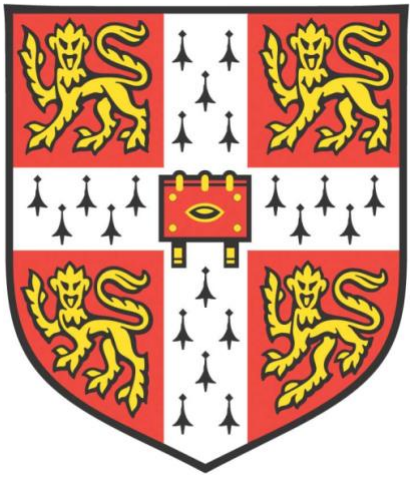
CONFLICT AND ADAPTATION: IDENTIFYING THE MARKERS OF COGNITIVE CONTROL IN THE TRANSITION FROM WAKEFULNESS TO SLEEP



ALEJANDRO EZQUERRO-NASSAR

QUEENS' COLLEGE

CONSCIOUSNESS AND COGNITION LAB,
DEPARTMENT OF PSYCHOLOGY

UNIVERSITY OF CAMBRIDGE

This dissertation is submitted for the degree of Doctor of Philosophy

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A mi abuela

DECLARATION

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text.

It has not been previously submitted, in part or whole, to any university of institution for any degree, diploma, or other qualification.

In accordance with the Degree Committee for the Faculty of Biology guidelines, this thesis is does not exceed 60,000 words, and it contains less than 150 figures.

Alejandro Ezquerro-Nassar

Cambridge, March 2021

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As this PhD comes to an end and I reach through the over-caffeinated, sleep-deprived fog that is my feelings, I find an overwhelming sense of gratitude towards all the people who have shared this experience with me.

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SUMMARY

Conflict and Adaptation: Identifying the markers of cognitive control in the transition from wakefulness to sleep

This thesis aims to investigate the cognitive changes that follow the transition from wakefulness to sleep. All studies presented have been driven by the hypothesis that consciousness is selectively required for some cognitive processes and not others. As such, fluctuations in alertness are hypothesised expected to produce a larger effect in those processes that are more reliant on consciousness.

In chapter 2 we begin by investigating the effect of alertness on conflict monitoring. Conflict monitoring is the environmental scanning process by which the brain detects conflicting information and identifies the need for top-down behavioural control. Using a combined Go/NoGo and Go-left/Go-right paradigm, we investigated effects of alertness on reaction times and responsiveness. We revealed an interaction between the task requirement to monitor conflict (Go/NoGo) and the level of alertness. Crucially, the difference between both tasks was only observed in the later stage of drowsiness. This suggests that conflict monitoring is more susceptible to reductions in alertness.

Our results from Chapter 2 also provide further evidence for the ecological validity of the Hori scale as a way to classify of the sleep onset period into functionally meaningful sub-stages. However, manual scoring of trials is an arduous process subject to interrater variability. In order to overcome these limitations, we developed an automated algorithm to classify trials into 3 alertness categories using Hori stage principles. This microstaging method was published in the journal

Neuroimage (Jahannathan, Ezquerro-Nassar, et al., 2018) and is included in its published form.

The method in Chapter 3 was then employed in Chapters 4 and 5, where we investigated effects of alertness and sleep deprivation in an auditory Simon task. This research was published in Journal of Neuroscience (Canales-Johnson, et al., 2020) and the manuscript is included in this thesis. Participants attended two sessions in the lab and performed an auditory Simon task, after a night of normal sleep or a night of partial sleep deprivation. We hypothesised that conflict detection processes necessary for an immediate conflict effect would be preserved under drowsiness, in line with studies showing residual processing for local, short stimuli during early sleep. Similarly, we predicted that sleep deprivation would not impair conflict detection.

Furthermore, we investigated the capacity to modify behavioural control using information from the previous trial via top-down mechanisms, known as conflict adaptation. The process that mediates the conflict adaptation effect is hypothesised to require consciousness. Therefore, we hypothesised that trial-by-trial conflict adaptation would be impaired during drowsiness and sleep deprivation.

In Chapter 4, we confirmed our hypothesis that the conflict detection is preserved under drowsiness, as indicated by slower reaction times for incongruent stimuli. However, we revealed an interaction between alertness, previous trial congruency and current trial congruency, suggesting a deleterious effect of drowsiness on conflict adaptation. At odds with our hypothesis, sleep deprivation was found to have a main effect on reaction times but it did not interact with any of the variables.

In Chapter 5, we found an increase in theta power associated to incongruent trials, a classic neural marker of cognitive control. This effect was observed during wakefulness but not during drowsiness, suggestive of potential alternative mechanisms underlying cognitive control under reduced alertness.

Overall, the findings of this thesis suggest that alertness has a different bearing depending on the cognitive process required. This has wider implications for the functional role of consciousness and suggests that sleep onset period is a useful framework to evaluate theories of consciousness.

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List of Abbreviations

ACC	Anterior cingulate cortex
AIC	Akaike information criterion
ANOVA	Analysis of variance
AUC	Area under the curve
BIC	Bayesian information criterion
DLPFC	Dorsolateral prefrontal cortex
DOC	Disorder of consciousness
EEG	Elelectroengephalography
ER	Error rate
fMRI	Functional MRI
GWT	Global workspace theory
HOT	Higher order thought
ISI	Interstimulus interval
LRP	Larteralised readiness potential
MEG	Magnetoencephalography
MRI	Magnetic resonance imaging
MVPA	Multivariate pattern analysis
N1	NREM sleep stage 1
N2	NREM sleep stage 2
NREM	Non-rapid eye movement
REM	Rapid eye movement
rmANOVA	Repeated measures ANOVA
ROI	Region of interest
RT	Reaction time

SEM	Standard error to the mean
SVN	Support vector machine
SWS	Slow wave sleep
TF	Time-frequency
ToC	Theory of consciousess
VS	Vegetative state
WM	Working memory

1

General Introduction

1.1 Defining the explanandum: why is the easy problem of consciousness so hard?

Consider for a moment the unique situation you find yourself in. The experience of *being* a self, possessing of agency and a sense of freedom, located within a world of objects that evoke personal meanings and sensations. Maybe some of these objects trigger memories, themselves linked to pleasant or painful emotions. This seamless process of association comes effortlessly to us in what is referred to as *the stream of consciousness*. We are blissfully blind to the intricate brain process of construction inherent in such subjective experiences, so our perceptions of the world present themselves as self-evident. Herein lies the danger of confusing the access to our own consciousness with access to *the processes* that give rise to consciousness. Arguably one of the main challenges when devising a science of consciousness is the ease with which we end up mistaking our conscious intuitions for knowledge *about* the nature of consciousness (Metzinger & Windt, 2015).

The debate around consciousness is murky and plagued with traps of intuition. Chalmers (1995) famously distilled the question into the hard and the easy problems of consciousness. By *easy problems*, he was referring to the set of questions that can be directly investigated by cognitive scientists, such as the study of information integration, the focus of attention, reportability of mental states, the differences between wakefulness and sleep, among others. The *hard problem of consciousness* –according to Chalmers— relates to the question of phenomenal experience. In his view, explaining how phenomenal consciousness emerges is beyond the scope of the scientific method.

Nonetheless, cognitive neuroscience has pushed forward into the so-called easy problems, to the full realisation that they are only easy by comparison. Arguably, some of the most difficult challenges are conceptual rather than technical, with no shortage of theoretical frameworks for conceptualising consciousness. So far, the approach has been to start at the level of subjective experiences and subsequently come up with biological theories that can account for the existence of such experiences and bridge the so-called "explanatory gap". This has led to an explosion in theories of consciousness (ToCs). Doerig et al. (2020) suggest that such a proliferation of theories is due to a lack in criteria about what constitutes a good ToC, but nonetheless agree that the processes which give rise to consciousness can be studied empirically. Indeed, they argue that is precisely empirical data that should be golden standard against which all ToCs are measured against, rather than their mere explanatory lure.

1.2 Content and State: the Yin and Yang of Consciousness Science

When Baars (1997) first articulated the Global Workspace Theory (GWT), he proposed that brain processes are akin to those of a theatre production, where most of the action occurs backstage and only the end product is on display. Going from

the assumption that consciousness arises as the result of information integration, GWT proposes that unconscious mental events occur at a local level up to the point where they become integrated and broadcast into the global workspace, giving rise to conscious experience.

In an effort to operationalise theoretical accounts of consciousness, researchers have typically differentiated between *contents* and *levels* of consciousness (figure 1D). Contents of consciousness closely resemble the philosophical concept of *qualia*, referring to those consciously accessible contents of the mind which are accompanied by phenomenal experience. On the other hand, the construct of *levels* of consciousness stems from the idea that consciousness is a graded rather than all-or-none phenomenon. In this view, sleep, vegetative state, comma, anaesthesia and wakefulness are some examples of different levels of consciousness (Overgaard & Overgaard, 2010).

More recently, Bayne et al. (2016) wrote against the conceptual utility of the construct of *levels* of consciousness, arguing that while it might be useful in clinical settings to classify consciousness alongside a single dimension, the notion of level can lead to problematic conclusions for the science of consciousness. Firstly, they argue, the idea of consciousness as graded phenomena seems to rely on the idea that level can be attributed on the basis of how vivid or clear the contents of consciousness are. However, this is more likely to be a measure of certainty, meaning that when a person reports the degree to which they perceived a content, they are in fact answering the question "*how sure am I that I perceived something?*". An intermediate level of certainty then gets equated with an intermediate level of consciousness.

A suggested alternative is that of conscious *states*, which differ on the ways in which they gate conscious content. Crucially, the notion of a state of consciousness does not imply linearity and by allowing states to vary across distinct dimensions lends itself better to scientific inquiry (figure 1A-C).

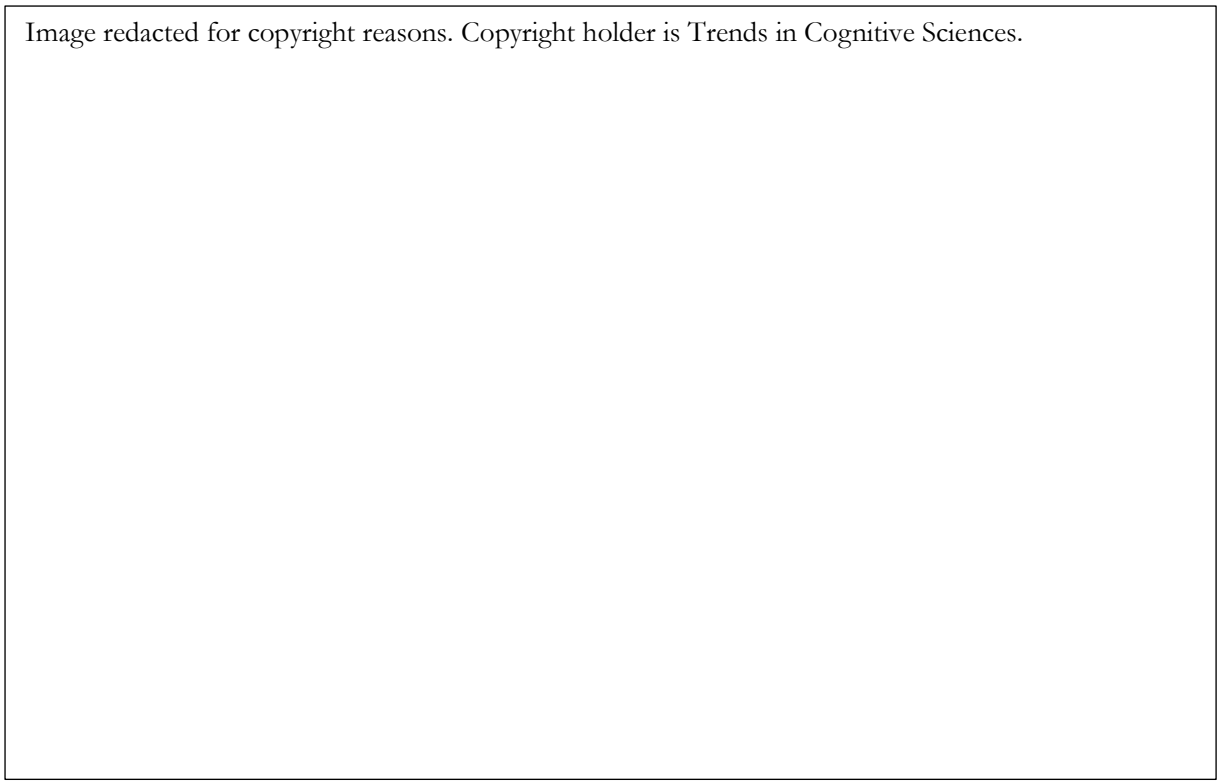

FIGURE 1. (A-C) SCHEMATIC REPRESENTATIONS SHOWING HYPOTHETICAL DIMENSIONS OF DIFFERENT STATES OF CONSCIOUSNESS. EACH DIMENSION REPRESENTED BY AN AXIS IS A HYPOTHETICAL PLACEHOLDER, TO BE REPLACED BY ANY MEASURE WE WISH TO USE IN ORDER TO CHARACTERISE EACH STATE. (A) EXEMPLIFIES A COMPARISON BETWEEN TWO GLOBAL STATES. (B) COMPARES DIAGNOSES AND OUTCOMES WITHIN A RELATED GLOBAL STATE. (C) REPRESENTS THE USE OF MULTIDIMENSIONAL FRAMEWORK TO CHARACTERISE INTERACTIONS BETWEEN TWO STATES. (D) FRAMEWORK SUGGESTED BY LAUREYS (2005), DESCRIBING CONSCIOUSNESS AS A FUNCTION OF TWO DIMENSIONS. FIGURE ADAPTED FROM BAYNE., ET AL. (2016)

1.3 What is consciousness for?

The functional question is concerned not with the biological processes that give rise to consciousness, but with the function of consciousness itself. In the last decades, it has become clear that a wide range of processes can be implemented outside of conscious awareness, to the point where it might seem like the existence of phenomenal experience is almost redundant. Indeed, in 1874 Thomas Huxley argued that consciousness is a biological epiphenomenon, arising merely as a neural by-product of evolution with no intrinsic function (Greenwood, 2010). In this view, consciousness is an inevitable result that accompanies certain behaviours but is not a necessity for the execution of such behaviours.

Epiphenomenal accounts of consciousness remain an unlikely possibility but are nonetheless difficult to disprove empirically. A more fruitful endeavour in cognitive science has been to identify the what functions of consciousness are and develop frameworks accordingly. A potential candidate for one of such functions is the control volitional action (James, 1890), where voluntary actions are preceded by a thought of performing that action. Moreover, those initiated actions can then be cancelled by voluntary inhibitory control (a volitional veto), thus exercising apparent "free will". This notion, whilst intuitively appealing, is heavily disputed in the literature.

Wegner (2004) proposed that the experience of volition comes as the result of inferences about mental causation whenever the action satisfies three conditions: primacy (the action was immediately preceded by *thinking* about the action), consistency (the action matches the thought), and exclusivity (the thought is the only explanation for the action). This view is supported by the existence of conditions such as alien hand syndrome, where patients limbs display apparent voluntary coordinated action that is nonetheless dissociated from the experience of volition.

This suggests that at least the experience of volition can be decoupled from volitional action.

Perhaps a more empirically testable claim about consciousness is that it enables flexible, context-dependent behaviour. Evidence suggests that consciousness is especially beneficial in the case of procedural learning, and that as new skills become integrated into procedural memory they become automated and less reliant on conscious access (Schneider, 2003). For example, a person learning to cycle might find themselves in their first attempt constantly rehearsing movements in their head, internally verbalising rules, and consciously monitoring their actions. With time, our cyclist will become less reliant on conscious monitoring and riding the bike will become an automatic skill.

1.4 Consciousness and cognitive control

Cognitive control refers to the ability of the cognitive system to flexibly adapt to sudden changes in task demands. It is a general term that encompasses multiple psychological processes, closely linked to philosophical notions of volition and free will. It has been suggested that some aspects of cognitive control can only be performed in the presence of consciousness, which would provide support for the view of consciousness as enabling volitional, flexible behaviour. Empirical evidence has thus far provided some support for this idea (for a review, see Kunde et al., 2003).

However, several forms of cognitive control have been found to occur outside of conscious awareness. For instance, Hughes et al. (2009) found that nonconscious primes during a Go/NoGo task modulate inhibitory ERP's, and furthermore that the extent of modulation was associated with subsequent performance. In another study, Jiang et al. (2015) found that a masked incongruent stimulus interfered with the performance in a simple button press task. In other words, conflicting information affected task performance and 6ehaviour6 with

stimulus processing even when unconsciously presented. A multitude of studies have shown similar results in processes such as task-switching (Reuss, et al.., 2011), conflict detection (Jiang, et al., 2015), motivation (Aarts, et al., 2008), error detection (Cohen, et al., 2009), and attention orienting (Ansorge and Neumann, 2005).

It has been suggested that the prerequisite of consciousness is determined by whether cognitive control is invoked by explicit or implicit events (Kunde et al., 2003). Explicit events are those where the stimulus contains direct information telling the participant what to do. For instance, in the case of a Go/NoGo task, a NoGo cue is explicitly mapped to the instruction that requires execution of inhibitory control. Other cases of explicit signalling include task preparation and attention orienting.

On the other hand, implicit events are those where the need for control can only be derived by integrating information from more than one explicit event and from the wider context of the task. Consider the Stroop task (Stroop, 1935), where participants are asked to name the colour of the ink in which a word is written while ignoring the semantic dimension of the word itself. On average, reaction times are longer for incongruent trials (e.g. correctly naming the ink as green when the word spells "YELLOW") than congruent trials (e.g. "GREEN" written in green ink). In this case, an implicit event would consist of manipulating an experimental block by increasing the frequency of conflict trials. In turn, this would provide information that, only if consciously detected, could be used to increase attentional resources and improve performance.

To test this hypothesis, Merikle and Joordens (1997) designed a variant of the Stroop task where prior to color stimuli (i.e. the sequence '&&&&&&&&' in either green or red ink), congruent and incongruent primes (the words 'GREEN' and 'RED') were presented either visibly or rendered unconscious by masking. When frequency of incongruent trials was increased, the Stroop effect was reversed and

participants performed faster for incongruent trials. Crucially, this was only the case when the primes were consciously available, but not when primes were masked.

(Gevers and colleagues (2015) further distinguish between bottom-up and top-down components of cognitive control. Bottom-up control is described as the "facilitated processing after repetition in responses and/or features of stimuli", whilst top-down components are those which involve "attentional reconfiguration on incongruent items." In order to investigate the effect of sleep deprivation on each of these components, they conducted a Stroop task where the words 'JAUNE', 'VERT' and 'ROUGE' (French for "yellow", "green" and "red") where presented in either congruent or incongruent colours of ink. Crucially, half of the incongruent trials were preceded by the same incongruent stimulus (e.g. ROUGE-ROUGE), and the other half of incongruent trials were preceded by a *different* incongruent stimulus (e.g. ROUGE-VERT). They found that a bottom-up effect of repetition was present in non-deprived participants, yet persisted after a night of total sleep deprivation, indicated by faster responses when the previous trial was incongruent and identical. Yet the top-down component of cognitive control was only observed in participants who had slept the previous night. This further demonstrated that trial-by-trial adaptation can be dissociable depending on the kind of control required.

1.5 Transitions of consciousness and the breakdown of cognition

Since the advent of human electroencephalography (EEG) more than 90 years ago, it has been recognised that electrical signals recorded from the scalp have a neural origin and therefore can be useful to determine biologically meaningful processes. Initially developed as a tool to study epilepsy, the potential for EEG was realised by sleep scientists as a powerful tool for probing into the proverbial "black box". In 1953, Kleitman and Asterinski described for the first time a series of stable time periods during sleep characterised by pendular or rolling movement of the eyes

accompanied by high frequency brain activity measured with EEG. This came to be known in the literature as rapid eye movement (REM) sleep, and thus the science of polysomnography was born. Dement and Kleitman (1957) then became the first to argue empirically for a link between EEG activity and subjective experience, reporting a high incidence of dream reports occurred during REM sleep.

Four other sleep stages of sleep have been proposed (figure 2), defined as Non-REM (NREM) stages 1, 2, 3, and 4 (further abbreviated to N1, N2, N3 and N4). Later, N3 and N4 were grouped into a single N3 stage (Silber et al., 2007) and this system has since been adopted by clinicians and sleep researchers alike to treat and understand sleep-related questions. Despite radical advances in the analysis of the EEG signal, the sleep scoring method has remained relatively unchanged ever since it was formalised by Rechtschaffen and Kales (1968).

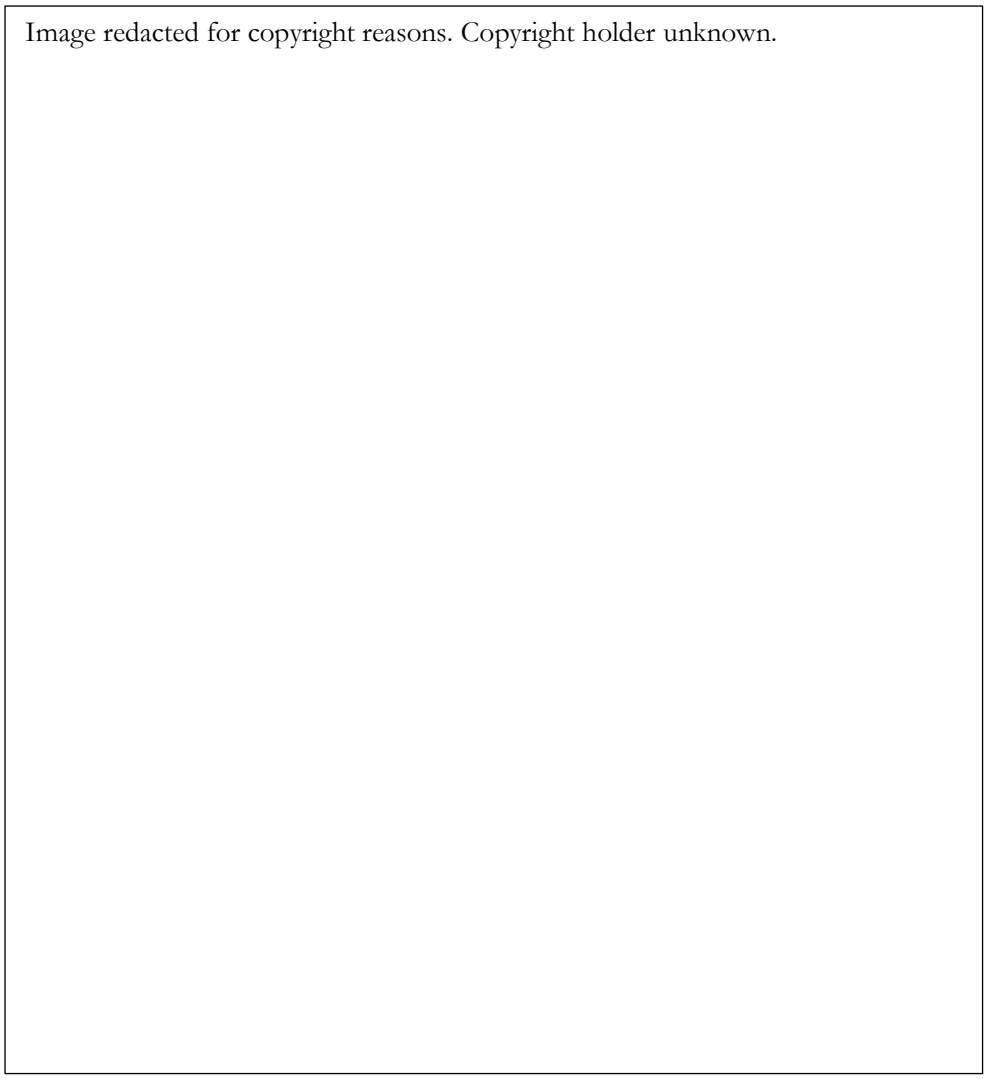

FIGURE 2. EXAMPLE OF STEREOTYPICAL EEG ACTIVITY DURING EACH SLEEP STAGE. (ADAPTED FROM HTTPS://WWW.HELPGUIDE.ORG/HARVARD/BIOLOGY-OF-SLEEP-CIRCADIAN-RHYTHMS-SLEEP-STAGES.HTM)

Typically, sleep scoring using PSG involves the breakup of the sleep EEG recording into 30 second time-windows, coupled with recording of muscle (electromyography; EMG), eye (electro-oculography, EOG), and heart (electrocardiography; ECG) electrical activity, as well as measures of respiration. Each 30-second epoch is then evaluated by eye and scored by one or two independent raters. This is an arduous process, nonetheless still preferred by many researchers despite some automated alternatives available. Furthermore, the use of

fixed 30-second epochs and the incorporation of only a handful of EEG electrodes is likely to provide an incomplete representation of brain activation during sleep.

This particular problem was recognised by Iber (2007) in the official guidelines for sleep scoring issued by the American Association for Sleep Medicine (AASM). Specifically, the sleep onset period (SOP) presents a challenge to the current scoring method due to its high heterogeneity and fast-changing dynamics (Hori, et al., 1994). When considering whether or not to include a category of drowsiness into the AASM guidelines, the scientific committee voted against doing so and instead opted to retain the original nomenclature, classifying wakefulness and N1 sleep as discrete stages.

Nonetheless, it is recognised that the transition from wakefulness to sleep is not a discrete process (with some exceptions, e.g. severe cases of narcolepsy), but a dynamic and gradual transition. This led Hori and colleagues (1994) to suggest that the sleep onset period not be evaluated under 30-second time windows, but using shorter 4-5 second windows in order to better represent the heterogeneity of the transition process. They put forward a classification system comprised of 9 stages in an attempt to encompass the full transition from wakefulness through to the beginning of N2 sleep (figure 3). Crucially, by dividing the EEG signal into shorter time windows the Hori-scoring method provides a slightly temporal resolution that can then be used to track the cognitive-perceptual changes associated with the SOP.

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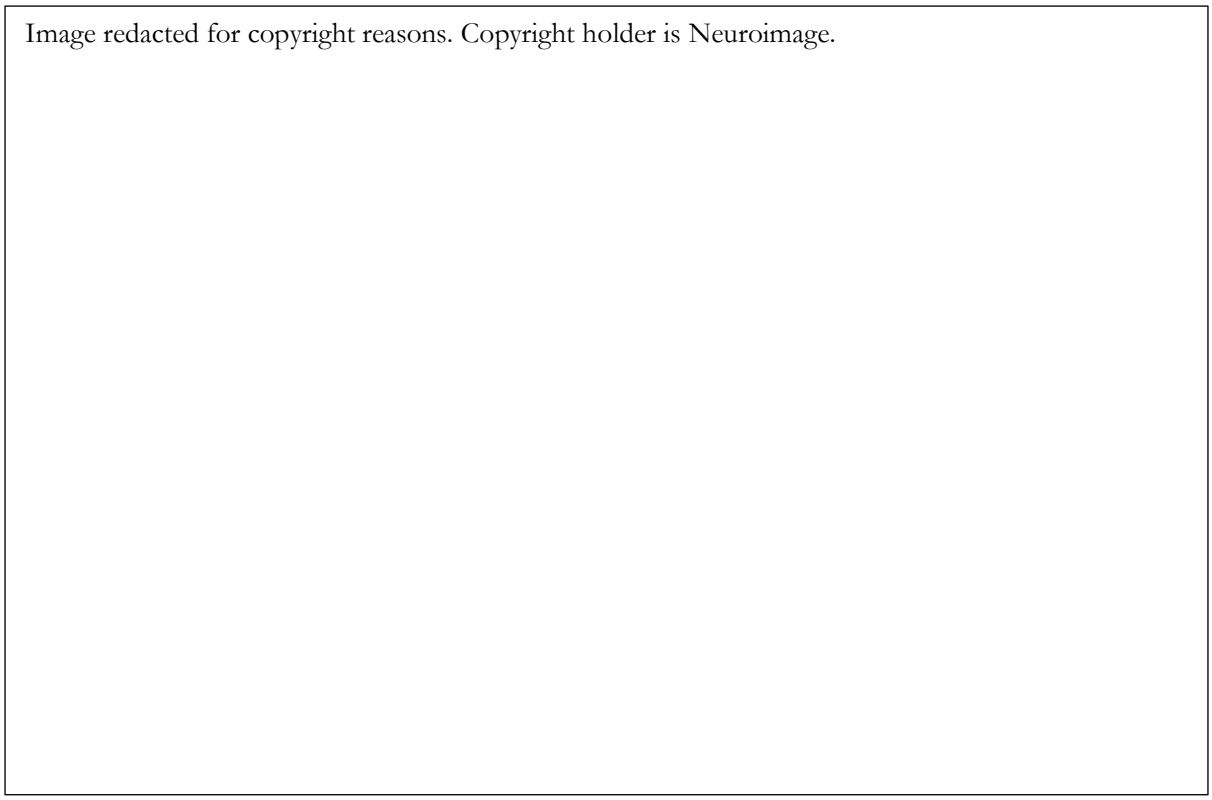

FIGURE 3. EEG ACTIVITY ASSOCIATED TO DIFFERENT ALERTNESS MICROSTAGES. COLOURED REGIONS INDICATE THE CHARACTERISTIC FEATURES OF EACH MICROSTAGE. ADAPTED FROM JAGANNATHAN, ET AL. (2018).

As Ogilvie (2001) has argued, understanding the SOP means understanding that there is no single "moment" of sleep onset. Rather, different neurobehavioural changes can be observed at different moments within the SOP (figure 4). To illustrate, one example of such changes comes from findings on auditory oddball paradigms (Winter, et al., 1995; Nittono, et al., 1999). Oddball paradigms consist of presenting a series of frequent identical tones with semi-randomly interspersed deviant tones (i.e. qualitatively different from the frequent tone). A signature of oddball paradigms is the resulting mismatch negativity (MMN) that comes from subtracting the frequent stimulus ERP from the oddball stimulus ERP, which is then used to infer whether or not the relevant sensory information was processed. Winter et al. (1995) found that MMN was still present during awake and N2 trials, but

changed during drowsy N1 trials, instead reflected by a broader fronto-central negative deflection. They speculate this to be reflective of a switch between environmental scanning mechanisms that occurs during drowsiness. This hypothesis remains an intriguing open question.

In a more recent study, Kouider et al. (2014) designed a semantic categorisation task where participants were asked to classify words into animal vs object categories. Surprisingly, LRPs typically associated with motor response planning were still observed during N1 and early N2 even when participants had become unresponsive. This demonstrated that semantical decision making and motor selection are preserved throughout N1 even after the loss of motor response.

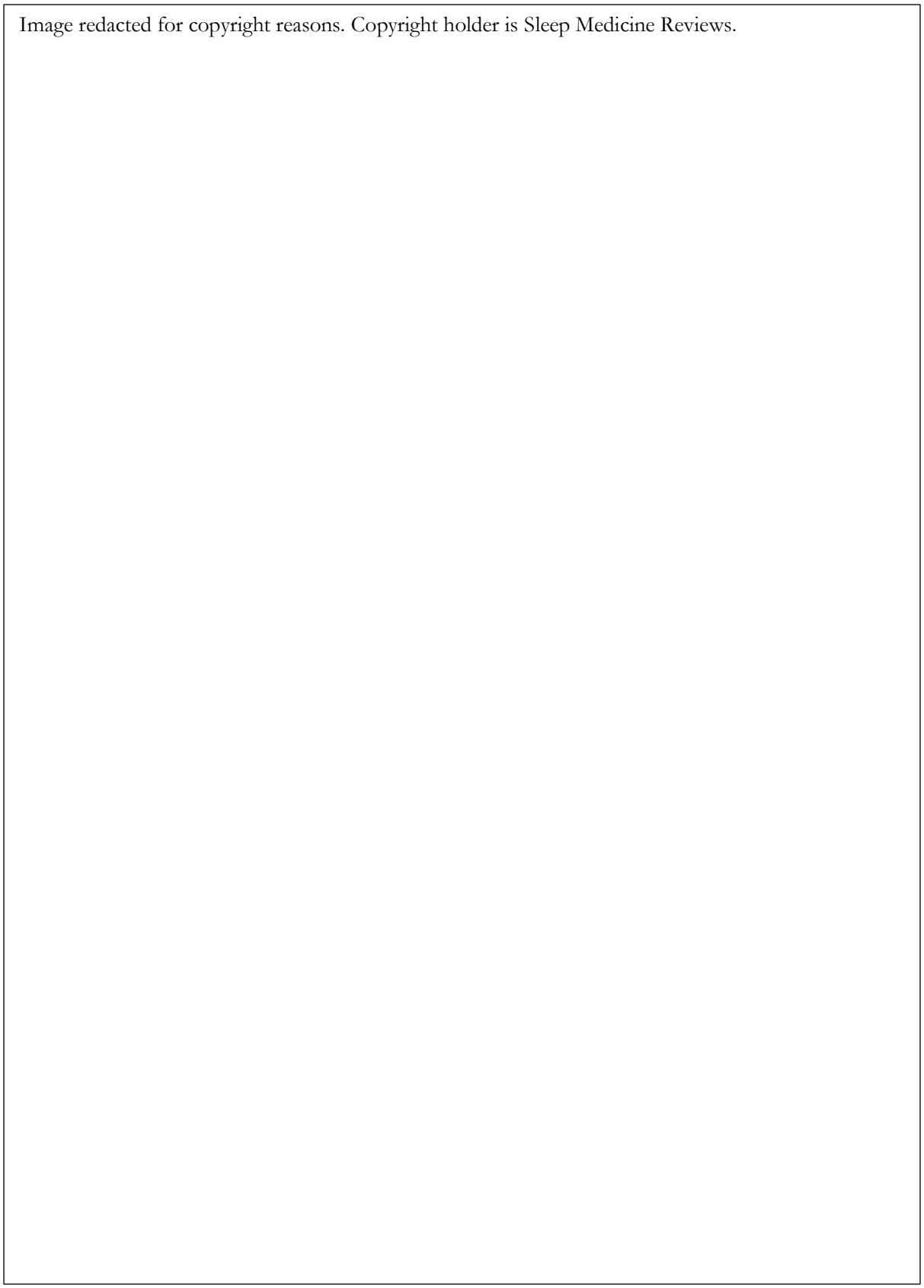

FIGURE 4. A BIOBEHAVIOURAL DESCRIPTION OF THE DYNAMIC CHANGES ASSOCIATED WITH DIFFERENT STAGES OF THE SLEEP ONSET PERIOD. ADAPTED FROM OGILVIE (2001).

The SOP is not only associated with distinct changes in cognitive processing, but also accompanied by distinct phenomenological experiences (Goupil & Bekinschtein, 2012), including the emergence of spontaneous, vivid imagery akin to dreaming. So-called microdreams (Nielsen, 2017) could provide a theoretical stepping stone in understanding how subjective phenomal experience shifts from external to internally generated, thus answering not only the question of how consciousness fragments but also how consciousness is reconstructed during sleep.

1.6 Sleep deprivation as it relates to conscious state and content

We began this introduction by asking '*what is consciousness for?'* We attempted to illustrate the difficulties that come with defining the question itself and the challenges of devising falsifiable hypotheses suitable for empirical study. In a parallel manner, biologists and cognitive scientists have attempted to answer the other side of the question (what is *sleep* for?) to moderately more success.

Tononi and Cirelli (2003; 2006) argue that sleep is (1) ubiquitous across animal species, (2) homeostatically regulated, and that (3) sleep deprivation comes at the cost of harmful consequences to the point of death (e.g. in sleep-deprived rats after 2-4 weeks). Dolphins are an interesting example, given that rather than evolving sleepless brains, they evolved a mechanism that enables unihemispheric sleep, during which they display a behaviour known as circular swimming. Altogether, it seems reasonable to suggest that sleep has an essential function across the animal kingdom.

Sleep is widely considered to be essential for processes involved in learning and memory consolidation. The synaptic homeostasis hypothesis (Tononi and Cirelli, 2003) suggests that neuronal synapses become potentiated during wakefulness as a result of new memory traces. The intensity of synaptic potentiation is directly related to the proportion of slow wave sleep (SWS) displayed during the

subsequent period of sleep. During SWS, synaptic weights are downscaled in order for new traces to become consolidated into long term memory.

Under the synaptic homeostasis theory, sleep deprivation is hypothesised to disrupt the homeostatic balance between synaptic strengthening and downscaling, resulting in the saturation of synaptic network connectivity, resulting in cognitive impairment (Niethard and Born, 2019). Furthermore, sleep deprivation has been found to reduce metabolic activity in prefrontal, parietal, and thalamic brain regions (Basner et al., 2013).

Interestingly, the study by Gevers, et al. (2015) described previously showed that it was specifically functions associated with frontal executive regulation of attention which become most affected by sleep deprivation. Slama, et al. (2018) conducted a simple study where they administered an N-back, Stop Signal and a cued match-to-sample task. Participants performed all three tasks, once after a night of full sleep, and a second time after a full night of sleep deprivation. They found impairments of sleep deprivation on task-goal switching and response inhibition, but preserved working memory (WM). This paints a mixed picture on effects of sleep deprivation on cognition and opens an avenue for future research to pinpoint precisely what are mechanisms through which sleep deprivation modulates cognition.

1.7 Summary

Thus far, we have outlined some of the difficulties encountered in the empirical study of consciousness. We have also delineated some of the frameworks developed over the past decades which have attempted to bridge the explanatory gap between phenomenal consciousness and its biological substrate, as well as established two key constructs in consciousness science: content and state. We have described how these constructs have informed the development of a science of

consciousness to the present moment, providing the framework for falsifiable scientific theories to be tested.

We then presented a brief historical background on the science of sleep physiology and addressed some of the pitfalls in sleep-scoring systems. Specifically, we argued that the classification of drowsiness and sleep into a single category is not representative of the unique neural-behavioural changes that occur during this period. We suggest that a sub-staging method proposed by Hori, et al. (1994) is a better tool to characterise the transition from wakefulness to sleep, and might provide new insights into the cognitive-conscious fragmentation processes underlying the transition.

Finally, we concluded by describing hypotheses of sleep function and its likely link to learning and memory consolidation. We further detailed how studies on sleep deprivation might shed light on the functional role of sleep, whilst revealing informative patterns about cognition.

1.8 Outline of Chapters

The purpose of this thesis was to shed light on the cognitive effects that follow the transition from wakefulness to sleep. The question we seek to answer is two-fold:

1) How does the gradual loss of alertness modulate cognitive control functions?
2) What forms of cognitive control might sleep be necessary for?

Our approach has been driven by the hypothesis that consciousness is selectively required for some cognitive processes and not others. Therefore, fluctuations in alertness (a linear dimension of consciousness) were expected to produce a larger effect in those processes that are more reliant on consciousness.

In chapter 2 we begin by testing the ecological validity of a still relatively unexplored scale (Hori) as a way to classify of the SOP into functionally meaningful sub-stages. Based on our Hori classification we derived 3 different categories of alertness as participants performed either a Go/NoGo task or a simpler Go-left/Go-right task. We hypothesised that responsiveness and reaction times would be more affected in those trials where conflict monitoring is required (i.e. the Go/NoGo task), providing evidence that cognitive control is more susceptible to the effects of reduced alertness than simpler semantic decisions.

To overcome the limitations of manual Hori scoring, we developed an automated algorithm to classify trials into 3 alertness categories using Hori stage principles. This microstaging method was published in the journal Neuroimage (Jahannathan, Ezquerro-Nassar, et al., 2018) and is included as a manuscript.

The method in Chapter 3 was then employed in Chapters 4 and 5, where we investigated effects of alertness and sleep deprivation in an auditory conflict task. We hypothesised that immediate conflict would still be detected and resolved under drowsiness (i.e. unaffected by reductions in alertness). On the other hand, we hypothesised that trial-by-trial conflict adaptation would be impaired during drowsiness. Chapter 3 is concerned with the behavioural findings of the study, while Chapter 4 addresses the modulatory effects of alertness and sleep deprivation on conflict-related theta power, a well-established EEG marker of cognitive control.

2

The effect of Drowsiness on Conflict Monitoring

In this chapter, I present the results from a study investigating the effect of alertness on two different decision-making tasks. Two sets of participants (each n=30) performed one of either task 1 or task 2. Task 1 involved a simple go-left/go-right decision following the presentation of a tone sequence. Task 2 involved a similar presentation of tones but added a Go/NoGo criteria, thus imposing an additional constraint on the decision (i.e. a response inhibition criterion). Crucially, "go" trials in task 1 and 2 were perceptually equivalent, but differed in cognitive load. We reasoned that adding an extra criterion of response inhibition would increase the need for top-down cognitive control, thus making the decision more susceptible to fluctuations in alertness. Confirming this hypothesis, we found that an effect of drowsiness depended upon task instruction, as indicated by an interaction between alertness and task on responsiveness and reaction times. We conclude that decisions requiring cognitive control are more susceptible to reduced alertness than simpler auditory categorisation decisions.

2.1 Introduction

Cognitive control is a key executive process, underlying cognitive flexibility and behavioural adaptability to environmental change. Yet, while many evolutionary theories of consciousness argue that behavioural adaptability is also the main advantage consciousness (i.e. subjective experience), it has been shown that at least some components of cognitive control continue to operate outside awareness (Van Gaal, et al., 2012; Linzarini, et al., 2017).

Cognitive control is not a single function, but rather a group of goal-oriented processes ever-changing in line with task demands. Such processes include conflict monitoring and motor inhibition. Nigg (2000) suggested there are at least four types of inhibition, one of such being response inhibition, exemplified by the Go/NoGo task.

The Go/NoGo task involves the presentation of stimuli that indicating the participant whether or not to effect a predetermined motor response (i.e. 'Go' and 'NoGo' stimuli). In order to perform the task efficiently, there must not only be an activation of the motor plan, but simultaneously an activation for the alternative plan to inhibit the motor response. This entails that in order to perform a Go/NoGo task, it is necessary to keep mechanisms of conflict monitoring active across all trials and the motor plan selection either. This requires constant performance monitoring throughout all trials. Van Boxtel et al (2001) conceptualise this form of inhibition to be a non-selective, less complex than that required for interference suppression (e.g. a Simon task), which requires the selection of a response

Typically, Go trials are used as controls against which neural activity in the NoGo trials is compared. Using this strategy, a consistent negativity in the frontal EEG signal has been found for NoGo trials after 200-300ms (N2) followed by a positive ERP 250-500ms (P300) after the NoGo stimulus is presented (Enriquez-Geppert, et al., 2010). In this context, both the N200 and the P300 have typically

been interpreted as reflective of inhibitory activity. However this view has been put in question, by arguing instead that these components are instead the result of conflict monitoring (Enriquez-Geppert, et al., 2010; Chatham, et al., 2012; Donkers & Van Boxtel, 2004).

Donkers & Van Boxtel (2004) designed a set of sister tasks, conceived to differentiate the effects of inhibition against the effects of conflict monitoring. The first task consisted of a standard Go/NoGo while the second task (the "go/GO" task) required participants to effect either nominal or forceful responses to a stimulus. In both tasks, response cue was preceded by an arrow indicating whether to execute a left or a right response. Crucially, 'go' trial frequency for both tasks was set at either 50 or 80% in order to manipulate response bias. When 'go' trials were frequent (i.e. 80%), they found the N200 component was modulated 'NoGo' trials in the Go/NoGo task, but also by 'GO' trials in the go/GO task, indicating that N200 might not be a measure of inhibition but rather a measure of conflict monitoring. This suggests that 'go' trials in a Go/NoGo task are not exempt from the need of cognitive control, but rather inform behaviour and are themselves subject to conflict monitoring processes.

2.2 Research Question

This study seeks to address a general question: does alertness modulate conflict monitoring during a Go/NoGo task?

More specifically, we address the following:

1. Is responsiveness during a go/nogo task modulated as a function of alertness? We hypothesised that a task demanding top-down conflict monitoring and inhibitory preparation would result in reduced responsiveness during drowsiness, compared to the task where no such monitoring is required.

2. Is reaction time during a go/nogo task modulated by alertness? We expected that trials where conflict monitoring is required would result in higher RTs. Crucially, we also predicted an interaction would emerge between alertness and task, reflective a selective disruption of alertness on conflict monitoring.

2.3 Methods

2.3.1 Task

60 healthy participants (age range: 18-35) performed one of either a go-left/go-right task (n=30) or a go/nogo task. During the go-left/go-right task — referred from here onwards as the *go task*— participants listened to a series of tone pairs, where the first tone indicated whether to press a left or a right button. An inter-stimulus interval (ISI) of 1550ms was followed by a second tone, prompting participants to execute a response. Inter-trial interval varied from 5-12s. Participants were instructed to respond as accurately as possible and each session consisted of a variable trial number between 100-250.

Stimuli, ISI, and tone-response mapping in the GO trials for the Go/NoGo task were equal to those in the Go task. ITI also varied randomly between 5-12s. However, a second type of trial was introduced, requiring participants to inhibit their response in case of a mismatch between the sound of the first and the second stimulus (see Fig 5). During both tasks, participants were allowed to fall asleep but were awakened and prompted to continue if stage 2 was detected by eye (online) or if two trials were missed in a row. They were instructed to keep bodily movements to a minimum and keep the eyes closed throughout the experiment.

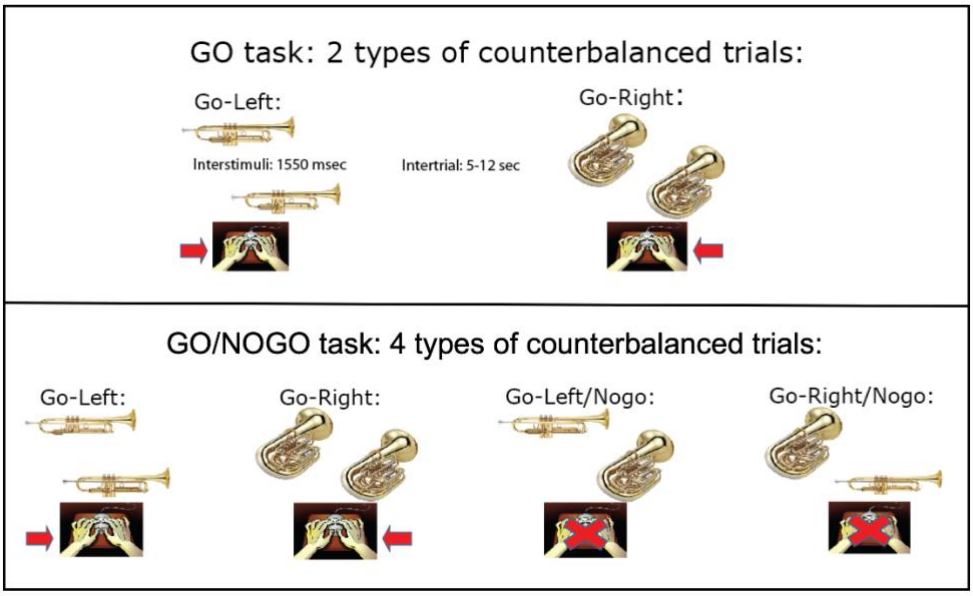

FIGURE 5. SCHEMATIC REPRESENTATION OF OUR GO AND GO/NOGO PARADIGMS. THE GO TASK REQUIRED PARTICIPANTS TO PRESS A LEFT OR RIGHT KEY CONTINGENT UPON STIMULUS 1. THE GO/NOGO TASK CONSISTED OF THE SAME SET OF STIMULI, BUT STIMULUS 2 ALTERNATED BETWEEN A 'GO' AND A 'STOP' SIGNAL, REQUIRING PARTICIPANTS TO EXECUTE OR INHIBIT A RESPONSE. 60 PARTICIPANTS WERE RANDOMLY SPLIT INTO EACH TASK (N=30).

2.3.2 EEG

Participants were fitted with an EGI electrolyte 62-channel cap (Neuroscan systems) after receiving the task instructions and subsequently signing an informed written consent form. EEG was sampled at 500Hz, then downsampled to 250Hz and high-pass filtered at 1Hz. Continuous EEG data was epoched at -5500 to 4000ms around second stimulus onset. Noisy channels where variance exceeded 500 were rejected and interpolated using spherical interpolation. Noisy epochs were removed by visual inspection, where frequency and/or amplitude in multiple channels exceeded that normally observed in brain activity (see appendix A). Finally contamination from eye movements and muscle artefacts was reduced using independent component analysis (Delorme and Makeig, 2004).

2.3.3 Alertness classification of EEG data

A method first suggested by Tanaka, Hayashi and Hori (1996), and modified by Goupil, Bekinschtein was used as a basis to classify the hypnagogic transition into 10 stages. The first two stages represent wakefulness, and are characterised by the amount of alpha activity (8-10 Hz) present in the EEG signal. Stages 3-4 represent early drowsiness (N1), and stages 5 onwards contain the features of deep N1 all the way into N2. Pretrial epochs from -4000 to 0ms were manually classified according to alertness level and then grouped into awake (Hori 1-2), mild drowsy (Hori 3-4) and severe drowsy (Hori 5-10). For a detailed description of the manual Hori scale classification method in full detail, see *Chapter 3*.

2.3.4 Statistical analysis

Responsiveness was analysed through a generalised linear mixed model (GLMM) using the presence-absence method described by Zuur et al (2010). Variance was modelled using a binary distribution and participant ID was used as a random intercept, and response was coded as a 0-1 variable, with 1 for response and 0 for no response.

For RT analysis, trials with RTs lower than 200 or higher than 3000ms were removed. Only Go trials were included in analysis and all types of errors were excluded. RTs were log transformed and analysed using a linear mixed effect model (LMM). Among other advantages, both LMM ang GLMM are robust to missing data and thus were optimal for our dataset, which is unbalanced in most of our predictor variables. Accuracy in the Go task (mean= 99.18%, SD= 1.27) and the Go/NoGo task (mean=98.21%, SD=2.72) were not further analysed, as performance was likely at ceiling.

As proposed by (Zuur, et al., 2010), we used a top-down approach to derive our best model for as follows:

1. Defined a model where the fixed parameters contain all explanatory variables of interest and their interactions. This is referred to as the *beyond optimal model*.

2. Used the *beyond optimal model* to optimise the structure for random effects in order the random components from containing information relevant to the fixed component of the final model. We used log-likelihood to choose our final random component structure.

3. Having found our optimal random structure, we then moved to determine the fixed component of the model. Here Zuur, et al. (2010) suggest reducing the fixed parameters by using the t-statistic. I.e. parameters with estimates with $p>0.05$ are removed in a stepwise manner and contrasted against the full model using the likelihood ratio test (LRT).

4. Once a final model was selected, we used restricted maximum likelihood (REML) estimates to redraw the final model structure.

5. We validated the RT model by plotting the distribution of its residuals on a histogram and visually assessed proximity to a normal distribution. The GLMM for responsiveness was validated by plotting the continuous predictor against the residuals.

2.4 Results

In order to understand the spread of our data across Hori stages, we first charted our total count of GO trials across participants in different Hori stages, regardless of responsiveness.

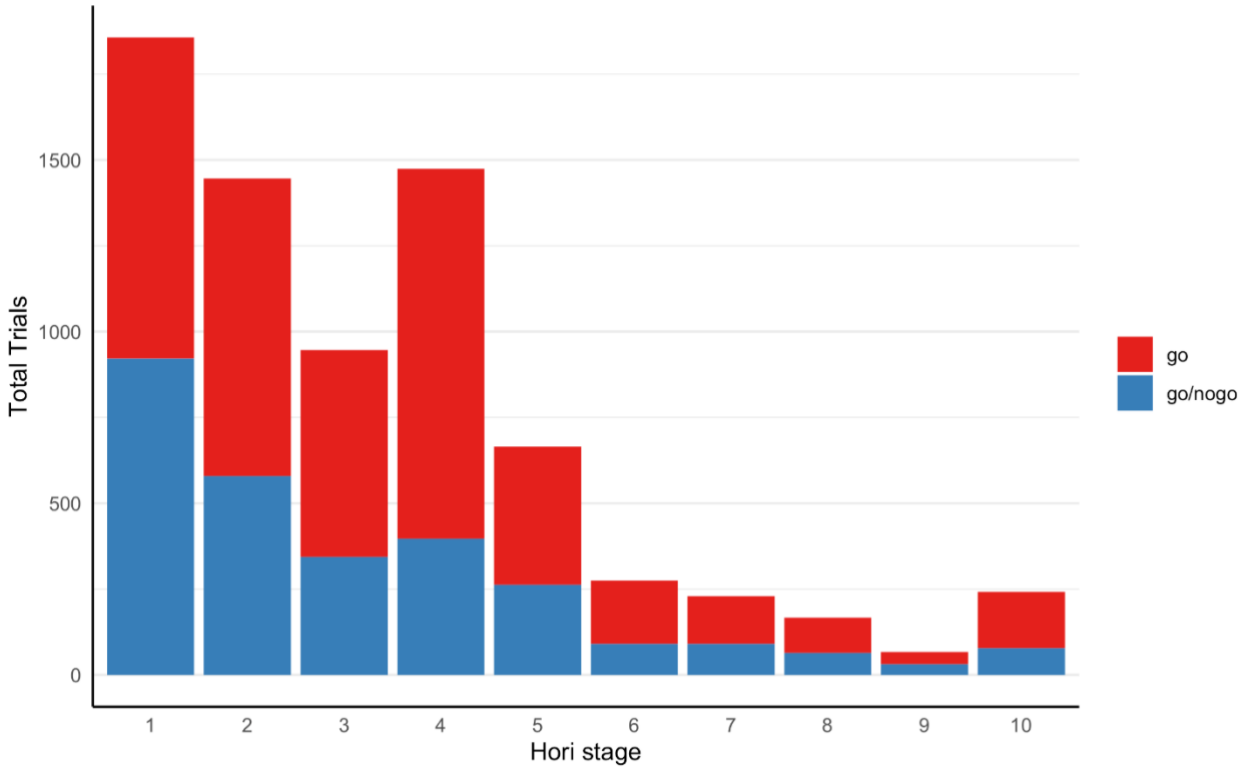

FIGURE 6. TOTAL NUMBER OF 'GO' TRIALS IN EACH OF OUR EXPERIMENTAL CONDITIONS DIVIDED ACROSS HORI STAGES.

As can be easily noticed in figure 6, trials in earlier Hori stages were much more prevalent than trials in late Hori stages. As such, we decided to group trials into 3 different alertness categories (figure 7):

(1) Awake: Hori stages 1-2

(2) Mild drowsy: Hori stages 3-4

(3) Severe drowsy: Hori stage 5-10

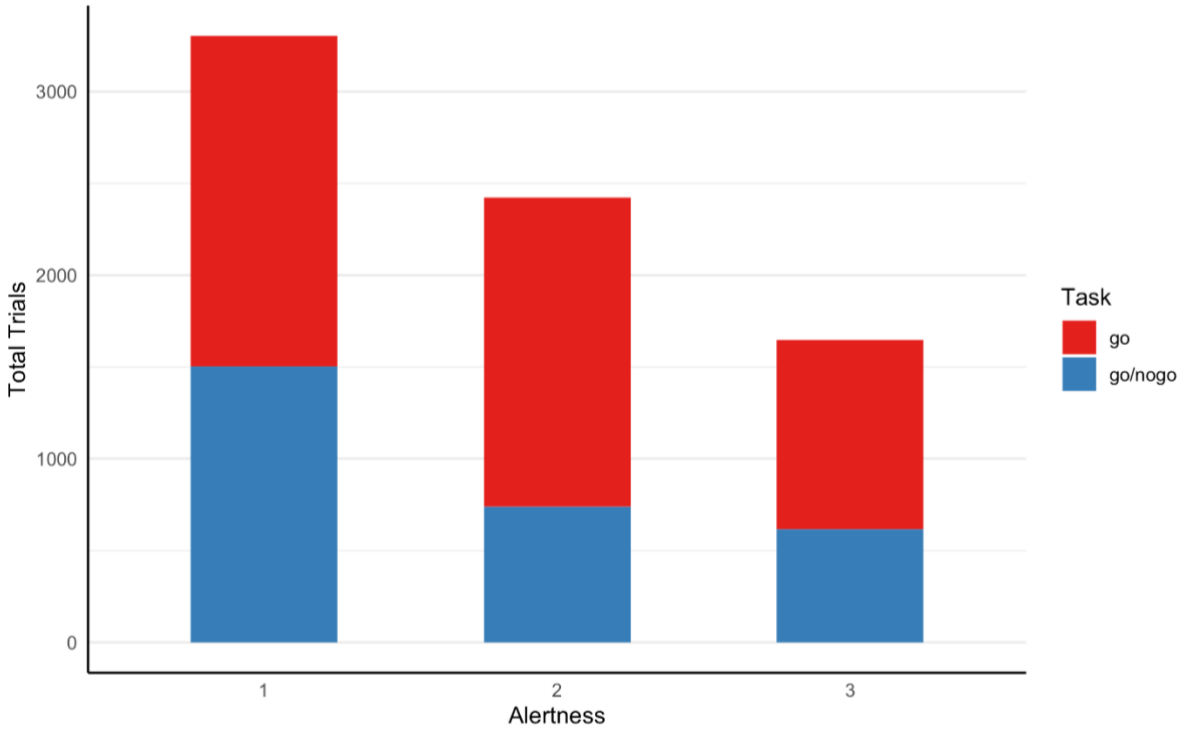

FIGURE 7. TOTAL NUMBER OF 'GO' TRIALS IN EACH OF OUR EXPERIMENTAL CONDITIONS DIVIDED BY ALERTNESS. ALERTNESS 1 REPRESENTS WAKEFULNESS (HORI 1-2), ALERTNESS TWO REPRESENTS MILD DROWSINESS (3-4), AND ALERTNESS 3 REPRESENTS SEVERE DROWSINESS (HORI 5-10)

After this newly defined alertness variable, we proceeded with our responsiveness analysis.

2.4.1 Responsiveness

After grouping trials in alertness groups 1-3, we analysed whether responsiveness during the task was associated to trial-by-trial levels of alertness we derived from our Hori scores. A look at individual participant data begins to show a trend, with seemingly more participants becoming unresponsive in alertness 3 for the Go/NoGo task (figure 9), compared to the Go task (figure 8).

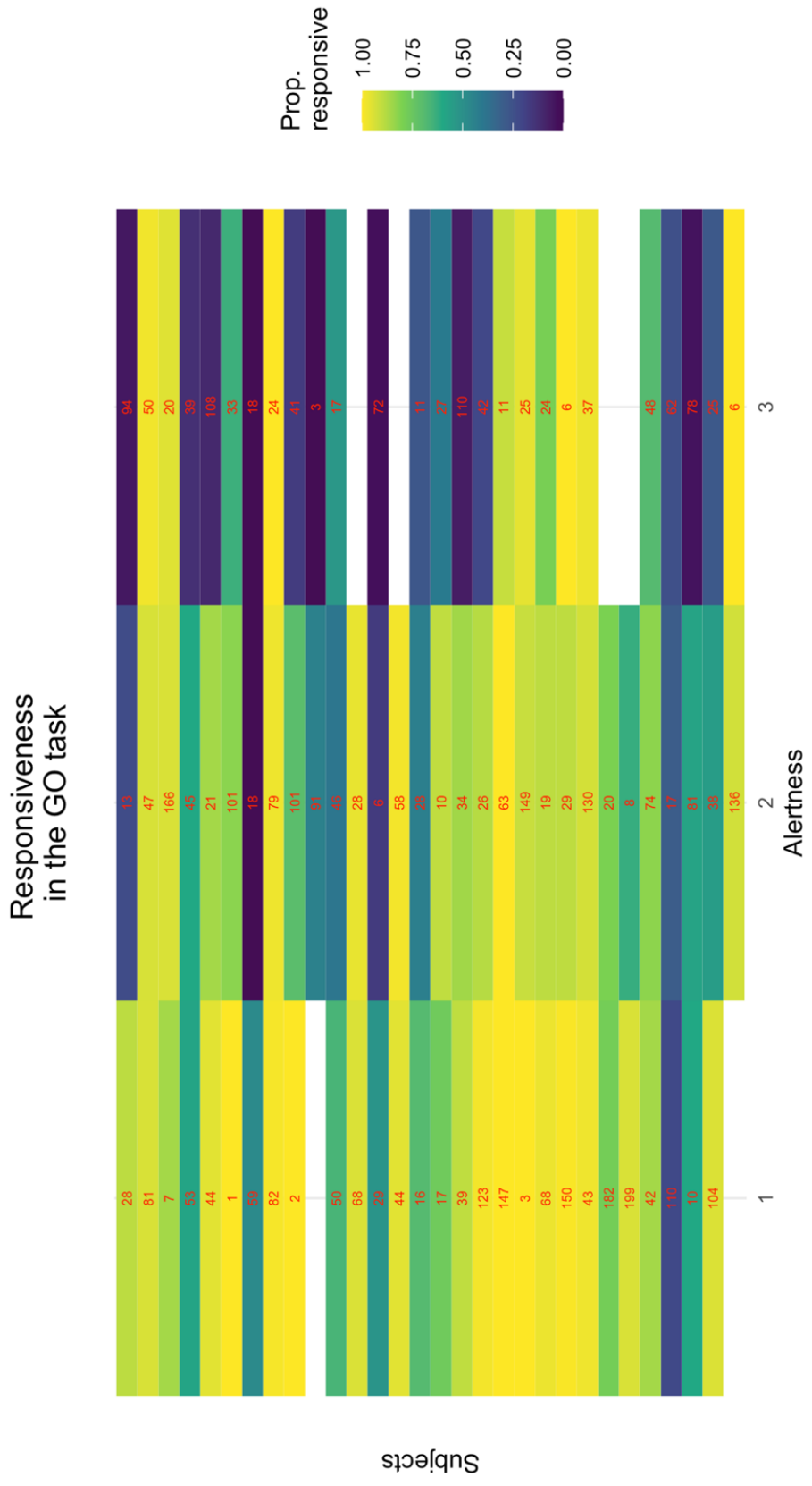

FIGURE 8. INDIVIDUAL RESPONSIVENESS ACROSS ALERTNESS LEVELS DURING THE GO TASK. NUMBERS IN EACH CELL REPRESENT THE TOTAL NUMBER OF TRIALS PER SUBJECT IN EACH CONDITION. EMPTY CELLS REPRESENT CONTITIONS WITH 0 TRIALS.

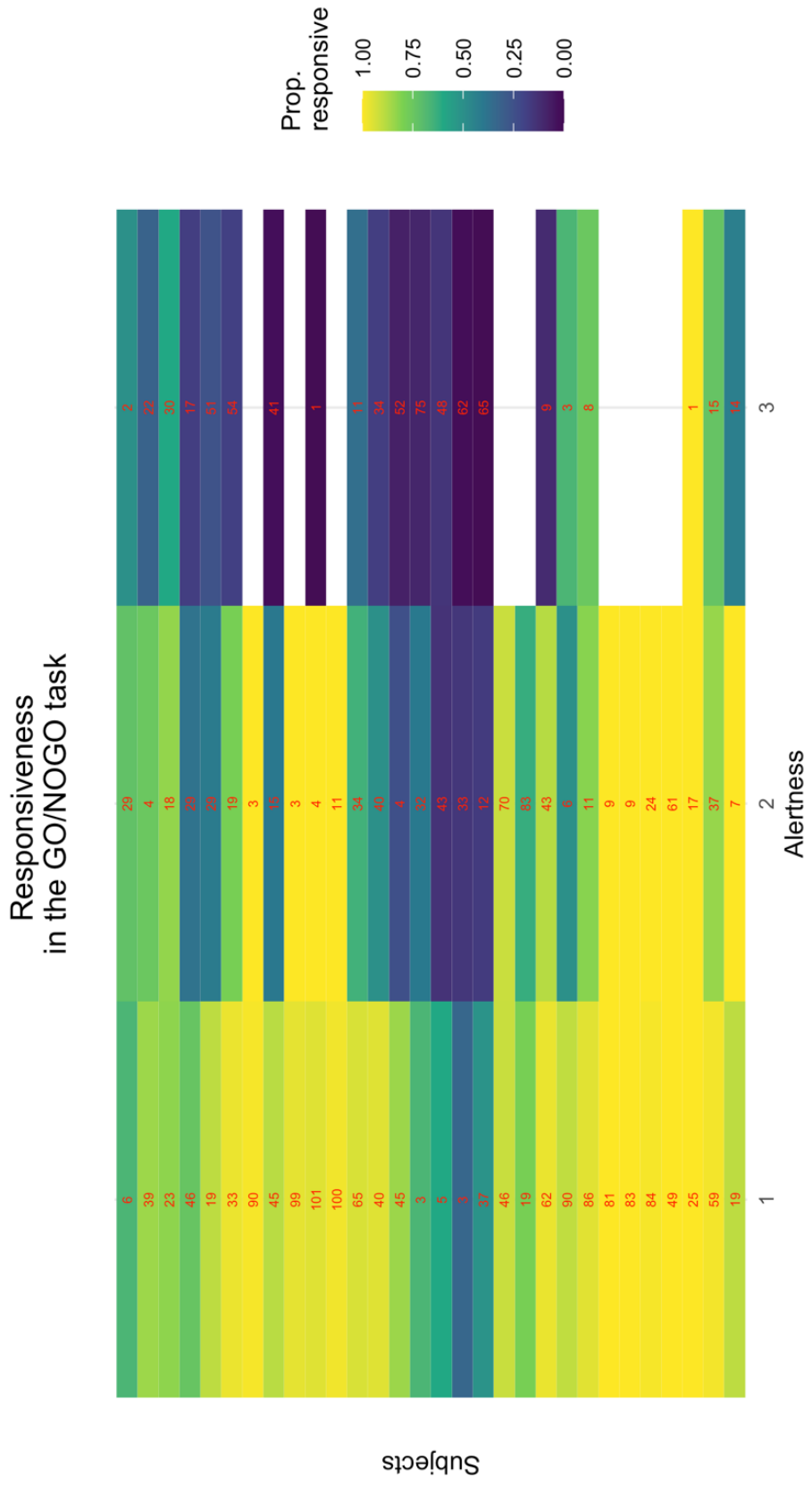

FIGURE 9. INDIVIDUAL RESPONSIVENESS ACROSS ALERTNESS LEVELS DURING THE GO/NOGO TASK. NUMBERS IN EMPTY CELLS REPRESENT CONDITIONS WITH 0 TRIALS.

A further look at group means in each task further revealed an interaction trend between alertness and type of task (figure 10).

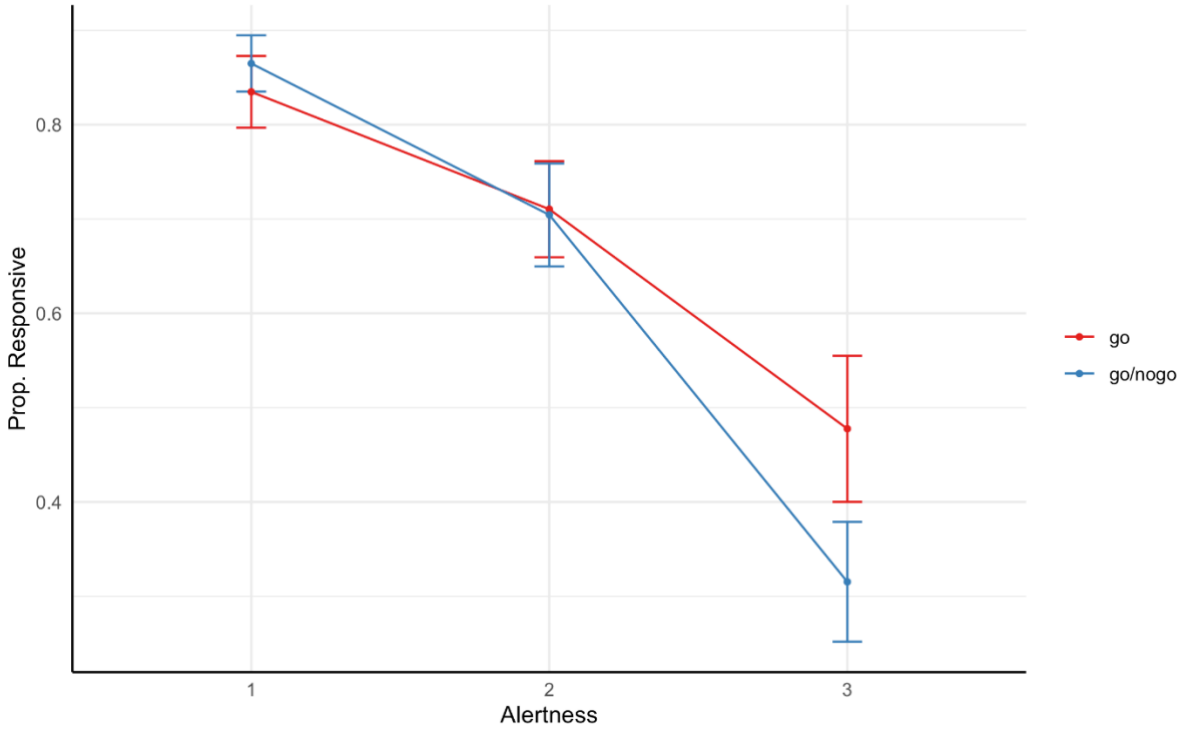

FIGURE 10. PROPORTION OF RESPONSIVE TRIALS IN EACH TASK ACROSS DIFFERENT LEVELS OF ALERTNESS. ALERTNESS 1 REPRESENTS THE MOST ALERT STAGES (HORI 1-2) AND ALERTNESS 3 REPRESENTS THE LEAST ALERT (HORI 5-10). SUBJECT-WISE AVERAGES WERE CALCULATED WITH BARS SHOWING SEM.

We proceeded to construct a GLMM with participant ID as random intercept. A presence-absence method for binomial distributions was implemented, following the top-down method suggested by Zuur, et al (2010). Our starting model was a task*alertness interaction with subject ID as random intercept. We found that this model was the most adequate in explaining responsiveness (table 1), supporting our hypothesis that a more complex task results in earlier loss of responsiveness. A post-hoc analysis revealed that a model including only task as fixed effect (BIC= 6205.5) was no better than our null model (BIC= 6214.0, p=0.523), suggesting no explanatory power of task alone and thus no effect of task.

TABLE 1. RESPONSIVENESS MODEL COMPARISON FOR THE GO/NOGO TASK

Model	Fixed Parameters	Random Parameters	Log-Likelihood	Pr(>X2)
Null	Mean	Intercept: ID	-3093.8	-
Task only	Task	Intercept: ID	-3093.8	0.5227
Alertness only	Alertness	Intercept: ID	-2568.3	<0.001
Independent effects	Alertness + Task	Intercept: ID	-2568.3	<0.001
Interaction	**Alertness*Task**	**Intercept: ID**	**-2557.5**	**<0.001**

2.4.2 Reaction Times

In order to explore the distribution of RTs across alertness, we first plotted the distributions of trials from all participants divided by task and alertness. Whilst no differences are noticeable in the awake condition, RT distribution begins to flatten and spread increases with alertness in the Go/NoGo condition. RT distribution in the Go condition appears to stay roughly the same across all alertness levels.

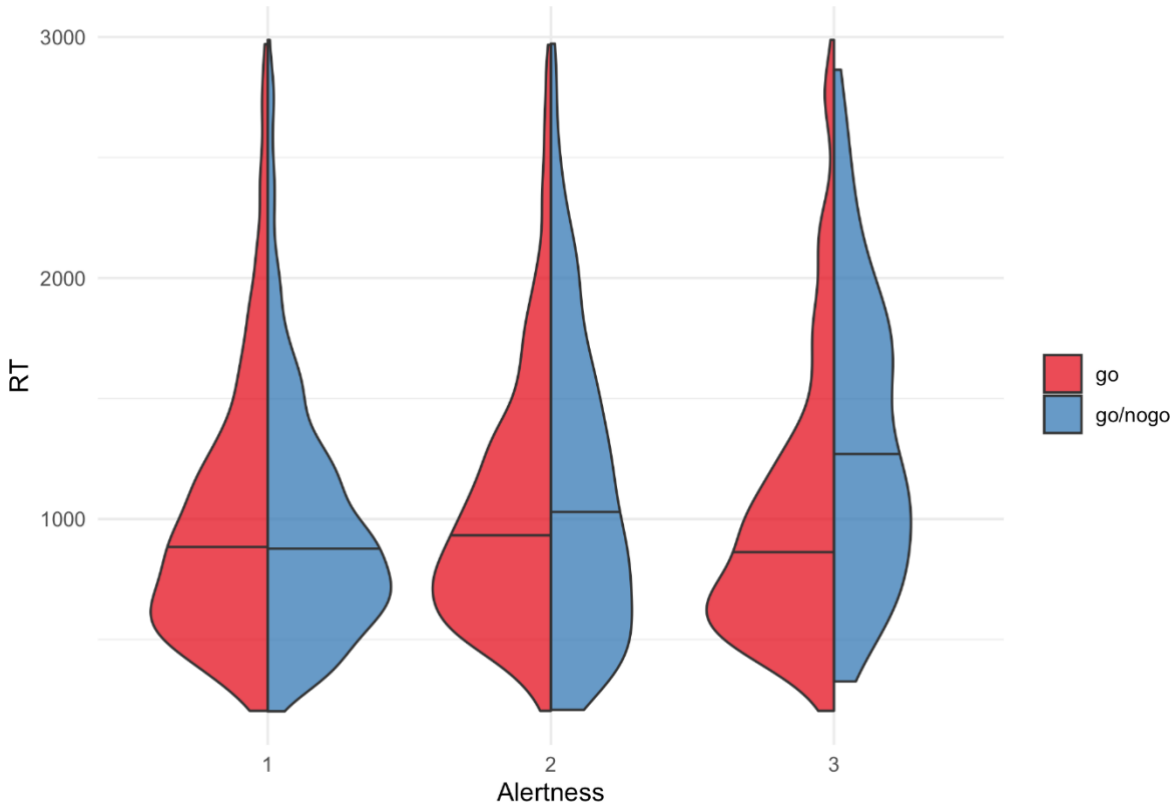

FIGURE 11. DISTRIBUTION OF ALL RTS COLLAPSED ACROSS SUBJECTS SHOWING A LARGER DRIFT IN THE GO/NOGO TASK THAN IN THE GO TASK . BLACK LINE INDICATES MEDIAN.

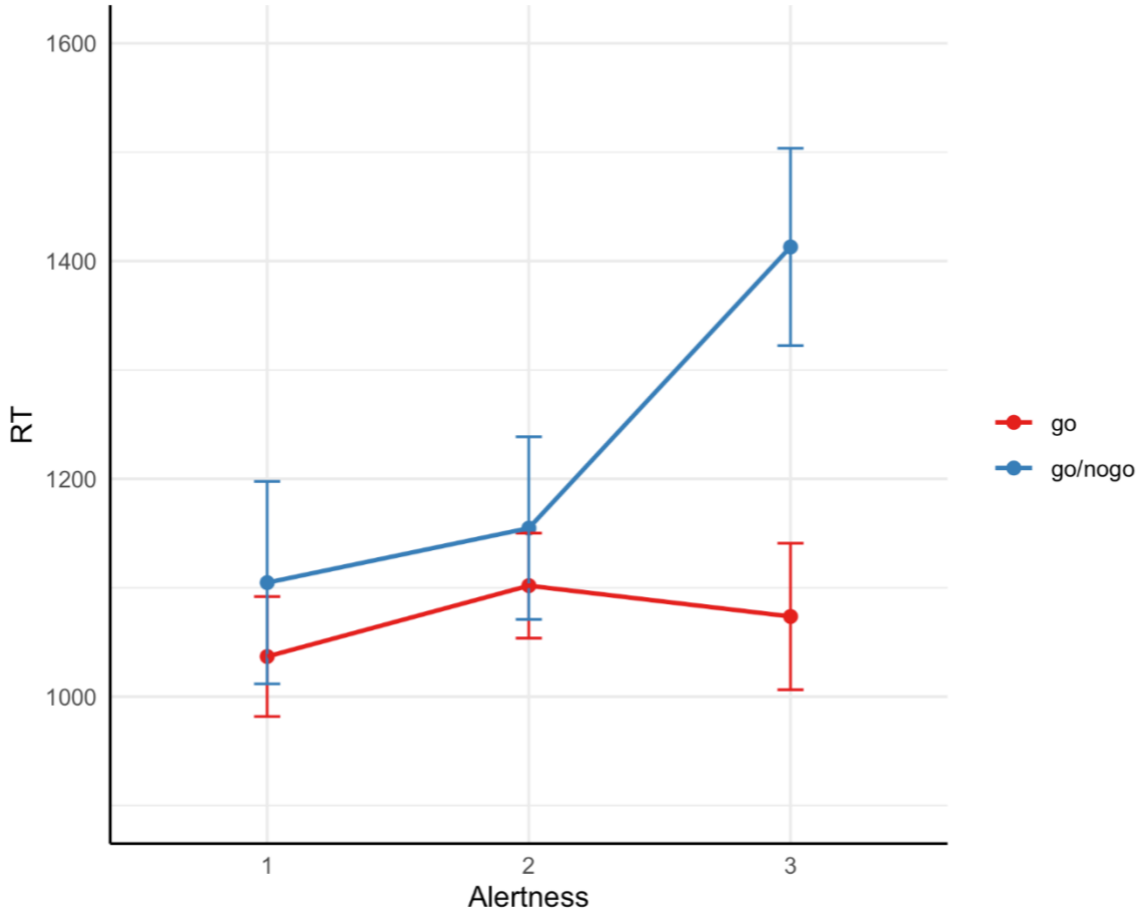

FIGURE 12. RT GRAND MEANS AT DIFFERENT ALERTNESS LEVELS (SEM BARS). A NOTABLE DIFFERENCE EMERGES BETWEEN TASKS AT LATER STAGES OF DROWSINESS. THIS SERVES TO ILLUSTRATE THE FINDINGS FROM OUR MIXED MODEL, INDICATIVE OF AN INTERACTION BETWEEN TASK AND ALERTNESS LEVEL.

To select our RT model, we began from the most complex model, also known as the beyond optimal model (Zuur, et al. 2010). Due to lack of convergence we could not model random slope and therefore kept only participant id as random intercept in our random effects component of the model. We proceeded to remove each fixed effect in a stepwise fashion. However, there was only need for a single step, as the task by alertness interaction effect was reliable ($F_{(2,5057)=}$ 17.38, $p<0.001$). The model also revealed an effect of alertness ($F_{(2,5057)=}$ 25.36, $p<0.001$) but no reliable effect of task ($F_{(1,60.8)=}$ 1.47, $p=0.231$).

A post-hoc comparison of estimated marginal means was conducted for single contrast between tasks in the 3 different alertness levels. This revealed a significant difference between the Go and Go/NoGo tasks only in the latest stage of drowsiness (alertness 3; mean=-0.25, SE=0.09, p=0.025) but no differences between Go and Go/NoGo tasks within alertness level 2 (mean=-0.01, SE=0.085, p=0.518), nor alertness level 1 (mean=-0.04, SE=0.083, p=0.475). In other words, differences between RTs in the Go task and the Go/NoGo task emerge during deeper levels of drowsiness.

2.5 Discussion

In this chapter, we investigated alertness as a modulator of conflict monitoring processes. We designed a pair of tasks that contained equivalent trials but varied in instruction: a Go task and a Go/NoGo task. Crucially, the Go/NoGo task required participants to monitor incoming information and prepare for inhibitory action. On the other hand, the Go task required participants to hold and execute a motor plan, with no inhibitory load.

It has previously been suggested that some forms of cognitive control might be one of the few processes that con only be performed in the presence of consciousness (Kunde, et al., 2012), and indeed that the ability to flexibly respond to environmental changes might be the reason why consciousness evolved in the first place (Baars, 2002). However, some components of cognitive control have been shown to persist in the absence of conscious awareness. This includes inhibitory control, which has been found to operate in the absence of consciousness, or more specifically the absence of conscious *awareness* (Van Gaal & Lamme, 2012).

We showed that while inhibitory control can still be executed under reduced levels of alertness, it comes at a price of longer cognitive processing. This suggests to us that even while inhibitory control might still be implemented in reduced states

of consciousness, it represents a heavier cognitive burden than simpler cognitive processes. As alertness continues to decrease, it appears that behaviour gets shut from the top-down. That is, cognitive control processes "shut down" before motor execution processes do.

A shortcoming of this experiment is the variable trial number across participants and conditions. Whilst statistical confounds such as missing and unbalanced data are controlled for by mixed modelling, it is possible that other confounds may have been introduced. For instance, it's likely that participants with more trials would experience higher demands on sustained attention, whilst more trials would also increase the likelihood of drowsiness. Therefore, the drop in performance observed during drowsiness could be the result of cognitive fatigue or boredom, rather than drowsiness per se. Further studies with balanced trial numbers could compare within-state changes in performance from early to late trials as a way to assess the role of cognitive fatigue.

3

Developing an Automated Method for Microstage Classification

As is clear from Chapter 2, trial-by-trial classification of alertness is a useful tool if one wishes to understand cognitive changes associated with the transition from wakefulness to sleep. Additionally, the differential effect of alertness as a function of task demand is an important consideration for those who wish to study processes unrelated to alertness in order to avoid potential confounds. Particularly, fluctuations in alertness have been found to be a confounding factor in a large number of resting-state studies, even those with blocks as short as 3 minutes (Tagliazucchi & Laufs, 2014). However, significant hurdles make trial-by-trial classification challenging for most experimental settings. Firstly, Hori staging by eye is time-consuming and therefore not feasible for most researchers to implement into their analysis pipeline. Second, rating trials by Hori requires training and is bound to the effects of human variability.

With this in mind, we set out to develop an automated trial-by-trial microstaging algorithm that reliably classifies trials into 3 alertness stages using variance and coherence masures, as well as incorporating the presence of sleep graphoelements (Jagannathan et al., 2018). This method presents several advantages for scientists interested in the study of transitional states, as well as cognitive scientists who wish to systematically remove drowsiness artefacts from their observations.

3.1 Declaration of Contribution

The following paper was published in the journal *NeuroImage* (2018). I contributed to the creation of the gold standard dataset by providing manual ratings for Hori stages across all trials in Dataset #1. I subsequently contributed to theoretical discussions during writing and provided continuous feedback on the manuscript until the point of publication.

3.2 Note on Examiner Comments

During the examination for this thesis, several minor inconsistencies which escaped peer-review were pointed out. Firstly, it was noted that the text description from figure 2 is inconsistent with the axis labels on figure 2B. The figure label should read "Biphasic consists of a sharp *positive* deflection followed by a *negative* one, whereas Monophasic consists of only a sharp *negative* deflection." Similarly, the graphoelement detector figure of the supplementary materials is incorrect. Figure 10A incorrectly states filtering was done between 2-6Hz, when it was correctly reported in the paper to be between 0.25-6 Hz.

A second error regarding predictor variance (p145 of the paper) was pointed out, where it seemed like frequency bands A and D used for predictor variance are overlapping. This is not the case. Rather, frequency band D was in fact 12-16 Hz, and not 2-6 Hz as is written on the paper. Finally, the electrodes on p142 appear to be lateralised in the case of the automated Hori scoring. However, this is due to a misleading graphical representation of the electrodes' location. They were in fact symmetrically distributed.

Regarding the use of different electrodes for the manual and automated scoring, there were multiple reasons for this approach. The manual hori scoring relied on the most common electrode arrangement used in sleep staging methods. However, being less constrained by convention with the automated method we sought to survey a wider area of scalp EEG. We also reduced the number of

electrodes in order to ease the computational burden of running the algorithm. Finally, it is important to clarify that trials were assessed as a whole, rather than with each electrode individually. This means that the presence of a signature graphoelement in just one electrode was sufficient to classify the whole trial into the corresponding microstage. In practice, however, it would be rare to observe a graphoelement appear just in one electrode, as they are normally spread across a number of proximal electrodes. Classification of each microstage was done in the hierarchical manner described in Jagannathan, et al. (2018).

Journal article redacted. Copyright belongs to Neuroimage.

4

Conflict Under Pressure: Investigating Reduced Alertness and Sleep Deprivation as Behavioural Modulators of Cognitive Control

In this chapter, I present behavioural results of 42 participants who performed an Auditory Simon task while transitioning between wakefulness and sleep, overlapping with data published in Canales-Johnson, et al. (2020). Subjects attended two morning sessions, one of which was preceded by a night of partial sleep deprivation (<4hrs of sleep). Firstly, we qualitatively assessed variability between subjects and individual differences in reaction times (RTs) and error rates. We then undertook a mixed modelling approach on RTs in order to better understand the relationship between alertness, sleep deprivation, current congruency and previous trial congruency on the conflict effect. EEG data was also collected and results are presented in Chapter 5.

This collaborative study was run across multiple labs and with the contribution of multiple lab members. Considering the richness of the data, we opted to publish a manuscript focused on the neural mechanisms of cognitive control under reduced alertness (led by Canales-Johnson) separately from the manuscript addressing the question of sleep deprivation, even though both datasets were collected in parallel. When defining the structure of this thesis, we considered adding the resulting journal article at the end as an appendix, in order to avoid confusion between methodologies followed. Of note, the thesis contains a re-analysis of the behavioural data using a statistical approach better suited to missing and unbalanced data: linear mixed modelling. This circumvented some of the limitations in the behavioural analysis from Canales-Johnson, et al. (2020) and revealed an unreported interaction effect between alertness and conflict adaptation.

Subsequently, the EEG pipeline was repeated as performed on the paper but incorporated the sleep deprived data into the analysis. For clarity, we adapted the methods from Canales-Johnson, et al (2020) into the chapter.

4.1 Declaration of contribution

I collected all of the normal sleep and the sleep deprivation data for this study with the assistance of Henry Wang, a part II student under my co-supervision. I assisted with the pre-processing of the EEG data and the microstaging technique. I contributed to discussions and provided continuous manuscript feedback up to the point of publication.

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4.2 Brief re-Introduction

Cognitive control is the ability to flexibly allocate mental resources in response to the demands of a task. This process is reliant –among other things– on the successful detection and resolution of conflict, followed by top-down modulation of behaviour (Botvinick & Braver, 2015). Conflict detection is thought to be mediated locally by the anterior cingulate cortex (ACC) and to require acute local brain activation for short term information maintenance (Jiang et al., 2015). On the other hand, the capacity to retain information from preceding conflict and adjust behaviour to the presence of conflict (i.e. conflict adaptation) is thought to require globally distributed brain networks for long term information maintenance (Mansouri et al., 2009).

Cognitive control has largely been investigated through so-called conflict tasks (e.g. Jiang et al., 2015; Kunde et al., 2003) where participants are asked to make decisions according to task-relevant cues while ignoring task-irrelevant dimensions. The task becomes more effortful when relevant and irrelevant domains are meaningfully related, given that task-irrelevant cues interfere with task-relevant cues when attempting to produce an appropriate response.

Consider Simon-type paradigms, such as the Stroop task. The conflict monitoring model (CMM) states that the triggering of cognitive control requires online conflict monitoring to detect incongruences between stimulus dimensions (MacDonald et al., 2000). This process has been hypothesised to rely on fast-decaying, local brain processes of conflict *detection* in the anterior cingulate cortex (Van Veen et al., 2001). On the other hand, conflict *adaptation* is thought to require durable and stable neural activation for information relay across multiple high-level cortical regions, with the dorsolateral prefrontal cortex (DLPFC) playing a regulatory role (Mansouri et al., 2009).

In line with predictions from the CMM, a study by Jiang et al. (2015) found that both instantaneous conflict and inter-trial conflict adaptation were associated

with medial frontal theta power modulations, regardless of conflict awareness. However, only conflict that was fully consciously perceived was associated with inter-trial conflict adaptation processes reflected by an increase in theta power in the DLPFC.

To this day, most studies investigating cognitive control as a function of consciousness have focused on the extent of conscious *access* to relevant and irrelevant stimulus dimensions in the awake state. On the other hand, fewer studies have investigated cognitive control as it relates to *state* of consciousness. This question is relevant if we wish to understand how conscious state modulates behavioural and neural markers of conflict and conflict adaptation. Thus, we set out to investigate the behavioural and neural markers of conflict in the transition from drowsiness to sleep, to test whether conflict effects under reduced alertness would follow a similar pattern to those observed in reduced awareness (Jiang, et al. 2015).

4.2.1 Sleep deprivation

Alertness and sleep deprivation are two powerful yet dissociable factors that modulate the state of consciousness. For instance, it has been shown that a night of sleep deprivation can result in increased euphoria the following morning and is argued by some to be the most successful form of antidepressant therapy (Dallaspezia & Benedetti, 2015). However, over time, sleep deprivation tends to increase pressure on the organism as it incurs homeostatic "sleep debt" (Borbély et al., 2016).

A second question relates to the effect that general disruption of prefrontal regions via sleep deprivation would have on conflict monitoring and adaptation. Sleep deprivation has been found to reduce activity on the fronto-parietal attention network (Ma, et al., 2015), including the prefrontal cortex (Ramdani et al., 2013) and ACC (Hsieh, 2007). Additionally, we have found that these networks become increasingly distributed when conflict is presented under reduced alertness (Canales-

Johnson, et al, 2020). Therefore, we hypothesised that sleep deprivation would disrupt the mechanisms enabling conflict detection and conflict adaptation, with the latter being the most disrupted.

Sleep deprivation can be thought of as a functional disturbance of the cognitive system akin to a reversible lesion, whereas changes in alertness microstates can be better understood as functional rearrangements of a healthy system. Studied in conjunction, sleep deprivation and drowsiness provide a framework to understand the interplay between state of consciousness and functional integrity of the brain. In line with previous reports from the WM literature, (e.g. Chee and Choo, 2004), we expect that sleep deprivation will impair the networks responsible for long term information maintenance required for conflict adaptation. However, under the assumption that conflict detection is a local process that occurs largely outside awareness, we expect conflict detection will not be impaired by sleep deprivation.

4.3 Research Question

This chapter seeks to address one general question: do sleep deprivation and drowsiness modulate the detection of conflict and adaptation to conflict?

More specifically, we wish to address the following questions:

1. Is the process of conflict detection modulated by alertness?
2. Is the process of conflict detection modulated by sleep deprivation?
3. Is the process of conflict adaptation modulated by alertness?
4. Is the process of conflict adaptation modulated by sleep deprivation?
5. Conflict detection is considered to be a local, mostly unconscious process, whilst conflict adaptation is thought to require consciousness and long-range connectivity. Do drowsiness and sleep deprivation selectively affect adaptation to conflict, whilst still allowing conflict detection processes?

We expected drowsy, sleep deprived and incongruent trials to be related to higher (i.e. slower) RTs. We expected to find an interaction between previous and

current trial congruency in the awake but not in the drowsy trials in both normal sleep and the sleep deprived conditions.

4.4 Methods

4.4.1 Participants

42 participants (20 females, age range: 18-30, mean age= 24.03) were recruited using the University of Cambridge online recruitment system (SONA). All participants were healthy with no auditory impairment, no history of psychiatric illness or head injury. Participants received monetary compensation upon completion of the second session. The study was approved by the local ethics committee of the University of Cambridge and all participants provided written informed consent after an explanation of the experimental protocol.

4.4.2 Behavioural paradigm

Participants performed an auditory version of a Simon task based on Pieters (1981) where recorded samples of a native English speaker saying 'left' or 'right' were presented to participants on the left or right ears, resulting in four categories (i.e. left congruent, left incongruent, right congruent, and right incongruent). A stimuli was considered congruent when the word meaning corresponded to its physical location (e.g. 'left' in the left ear) and incongruent when the opposite occurred (e.g. 'left' in the right ear). All four types of trials were presented equally often in a random order. Participants were asked to press a button with their left or right thumb to report the location specified by the stimulus (the words 'left' or 'right'), and ignore the physical location of the stimulus (left or right ear). Participants were instructed to perform the task as accurately and as fast as possible. There were

no practice blocks and no feedback on performance provided at any point during the task.

The time between a response and the following stimulus was randomly set between 2 and 2.5 seconds. The inter stimulus interval was set to 2 seconds in absence of a response within that timeframe. As a result, the inter stimulus interval could vary from 2 seconds (response absent) to 4.49 seconds (maximum response latency of 1.99 seconds + maximum response stimulus interval of 2.5).

Prior to testing, participants were instructed to get a normal night's rest on the night previous to testing. Testing began between 9am and 5pm and lasted approximately 3 hours. Upon arrival, participants were sat down in a comfortable adjustable chair in an electrically shielded room. Participants were fitted with an EGI electrolyte 128-channel cap (Electrical Geodesics, Inc. systems) after receiving the task instructions and subsequently signing an informed written consent. Task instructions were to respond as fast and accurately as possible, to keep bodily movements to a minimum and to keep the eyes closed throughout the experiment. Participants were asked to report their answers with their thumbs on two buttons of a four-button response box that rested on their lap or abdomen.

During the "awake" block of the experiment, participants were instructed to stay awake, but with eyes closed. The back of the chair was set up straight and the lights in the room remained on. This block contained 500 trials and lasted for approximately 25 minutes.

Following the awake block, participants then repeated the same task, but this time were allowed to fall asleep. The chair was reclined to a comfortable position and the lights were turned off. Participants were offered a pillow and blanket and were told that the experimenter would prompt them if they missed 5 consecutive trials. This part of the experiment consisted of 2000 trials and lasted for approximately 1.5 hours. At the end of the session, participants were sat upright, and the EEG cap was removed. Stimuli were presented using PsychToolbox

software on a MacBook computer and data were acquired using NetStation on a second MacBook computer.

4.4.3 Sleep Deprivation

In a counterbalanced manner, 25 participants from the normal sleep session attended the lab a second session where they were asked to sleep for no longer than 4 hours on the previous night. 5 participants who attended the sleep deprived session did not attend the normal sleep session. In order to monitor participants sleep hours, messages were sent throughout the night via email requiring them to respond. However, no independent verification was done to ensure participant reporting of time spent sleeping was accurate.

FIGURE 13. ***SCHEMATIC REPRESENTATION OF OUR EXPERIMENTAL PARADIGM. PARTICIPANTS WERE ASKED TO LISTEN TO THE WORDS "LEFT" AND "RIGHT" PRESENTED TO DIFFERENT EARS. THEY WERE INSTRUCTED TO LISTEN TO THE WORDS AND PRESS A BUTTON WITH EITHER THE LEFT OR THE RIGHT HAND, WHILE IGNORING THE LOCATION (EAR) WHERE THE WORD WAS PRESENTED FROM. THE TASK WAS SPLIT BETWEEN A SHORT (APPROX 20 MIN) "AWAKE" SESSION AND A LONGER (APPROX 90 MIN) "DROWSY" SESSION. FIGURE INITIALLY PUBLISHED IN CANALES-JOHNSON, ET AL (2020).***

4.4.4 EEG

Each experimental session lasted between 2-2.5 hours, during which 128-channel high-density EEG data were collected using EGI gel caps (Electrical Geodesics Inc., Oregon, USA). Data were recorded in microvolts (μV), sampled at 500 Hz and referenced to the vertex, using the Net Amps 300 amplifier (Electrical Geodesics Inc., Oregon, USA).

EEG pre-processing was done by means of custom-made MATLAB (R20126, The MathWorks, Inc.) scripts supported by EEGLAB (Delorme & Makeig, 2004). Data form 92 channels over the scalp surface were retained for further analysis (for more details on pre-processing, see Chapter 4). Trial-by-trial alertness was derived from these datasets as described in Chapter 3.

4.4.5 Behavioural Analysis

Trials were divided into awake or drowsy using the method described by Canales-Johnson, et al. (2020), included at the beginning of this chapter. The first trial of each block was discarded. Missed trials and incorrect trials were also removed from analysis, as well as trials with RT <200ms. For the conflict adaptation analyses, we included only trials where both previous trial and the current trial were correct.

We opted to analyse RTs by adopting a multi-level modelling approach. Mixed models allow for missing data, which allowed us to include all subjects in the analysis (n=42), as opposed to including only those who attended both sessions (n=26). Given that performance is likely at ceiling (and thus, biased toward positive values), we did not pursue any statistical analyses. RTs were log transformed after observing that residuals from our initial models did not resemble a normal distribution. See *Chapter 2* for a general overview of the model construction process.

4.5 Results

Participants performed an auditory Simon task in which they were asked to press a left or right button according to the meaning auditory stimuli (the words "left" and "right") while ignoring the physical location of the stimulus. Conflict was introduced by altering the location of the stimulus, making it incongruent with the meaning. A first-hand inspection of the data reveals an expected slowing down and increased variability in RTs related to drowsiness, as shown graphically by stereotypical participants in figure 14.

We hypothesised both drowsiness and sleep deprivation would be associated with slower responses, irrespective of the need for cognitive control. However, given that conflict detection has been found to be preserved at reduced levels of awareness (Jiang et al., 2015), we predicted that, similarly, conflict detection processes would be preserved under reduced alertness. On the other hand, we predicted that reduced alertness would impair processes involved in conflict adaptation.

We expected both conflict adaptation and conflict detection to be robust to sleep deprivation during wakefulness. However, in contrast to the normal sleep condition, we hypothesised that drowsiness in the sleep deprived condition would impair both conflict detection *and* adaptation.

4.5.1 Visual Assessment of Individual Variability

As we expected, participants exhibit a clear increase in RT variability when they become drowsy, as can be seen by the individual plots in figure 14. Drowsiness also seems to be associated with overall slower RT across most participants, in both our normal sleep and sleep deprived conditions (figure 15).

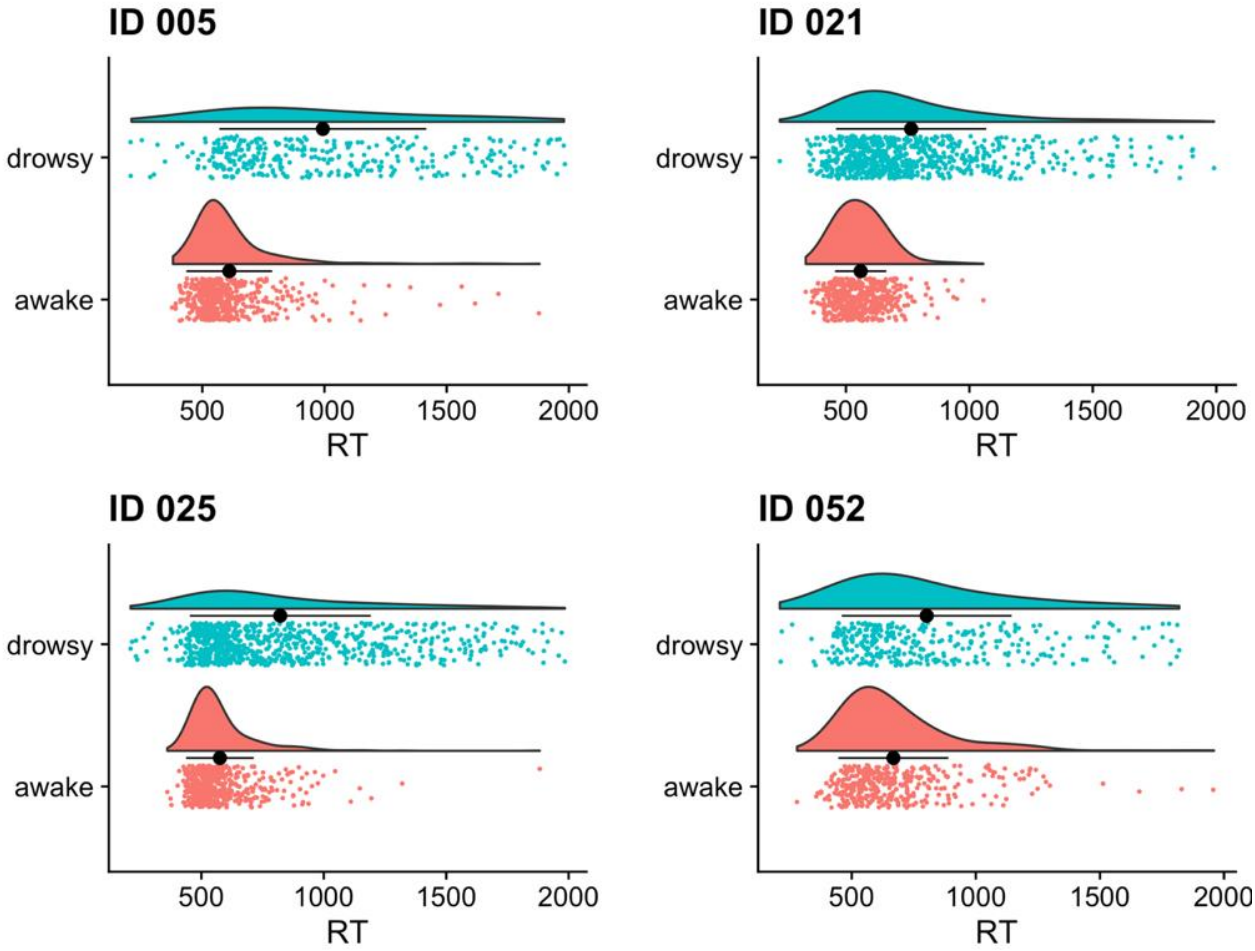

FIGURE 14. *RT DATA OF FOUR PARTICIPANTS SHOWING INDIVIDUAL VARIABILITY, AS WELL AS STEREOTYPICAL SLOWING DOWN AND "SPREADING OUT" OF RT DISTRIBUTIONS DURING DROWSINESS. EACH TRIAL IS REPRESENTED BY A COLOURED POINT, MEAN SHOWN BY BLACK DOTS WITH SD ON EITHER SIDES.*

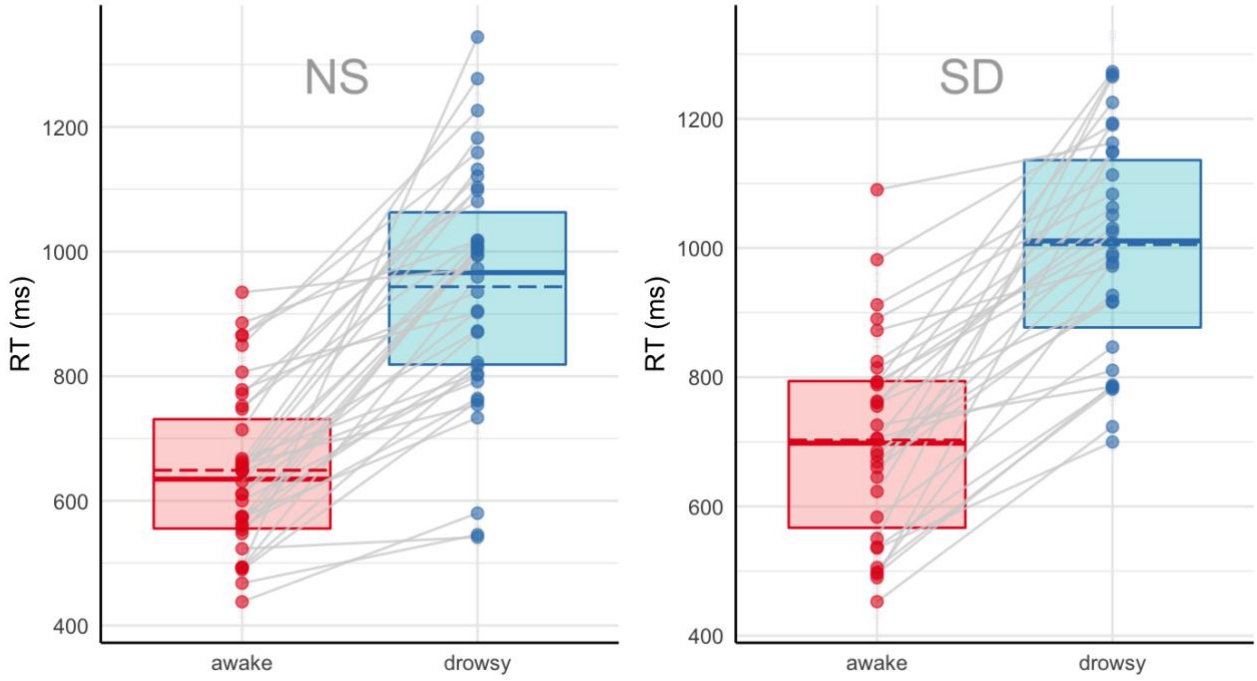

FIGURE 15. ***MEAN RTS IN PARTICIPANTS AFTER A NIGHT OF NORMAL SLEEP (NS) AND A NIGHT OF PARTIAL SLEEP DEPRIVATION (SD). EACH CONNECTED POINT REPRESENTS A PARTICIPANT, AND DASHED LINE INDICATES GRAND MEAN.***

Mean RT differences between congruent and incongruent trials of individual participants give a preliminary indication of a conflict effect, observed here as a trend towards slower responses for incongruent trials. Similarly, individual differences in error rates indicate more errors for incongruent than congruent trials.

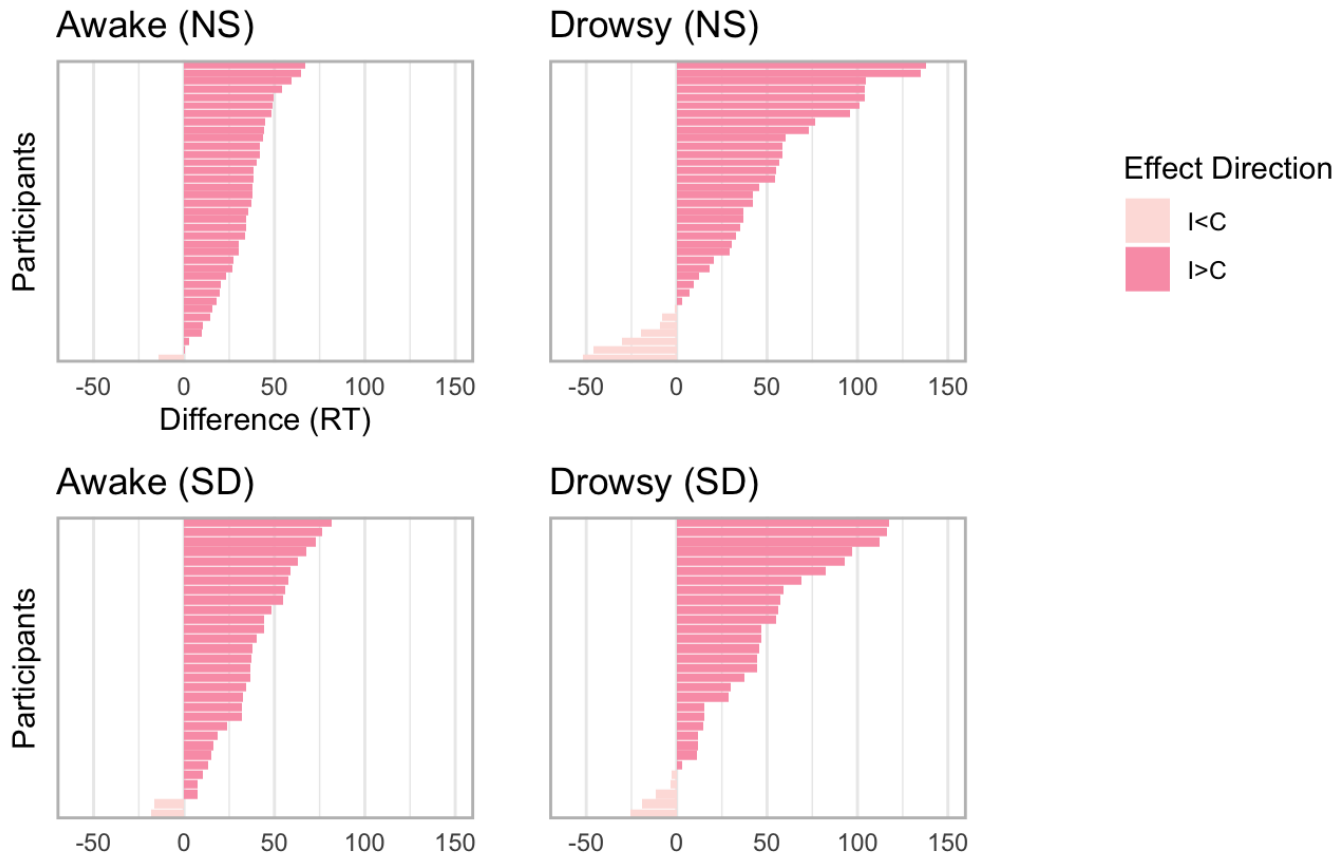

FIGURE 16. *INDIVIDUAL DIFFERENCES IN REACTION TIMES (RT) ACROSS SLEEP AND ALERTNESS CONDITIONS FOR ALL PARTICIPANTS. NS: NORMAL SLEEP; SD: SLEEP DEPRIVED*

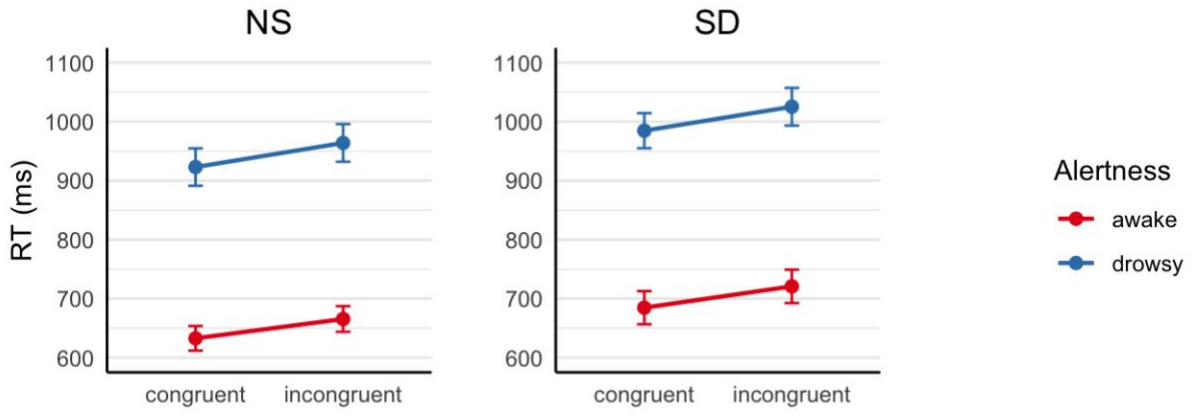

FIGURE 17. *RTS FOR CONGRUENT AND INCONGRUENT TRIALS IN PARTICIPANTS WHO ATTENDED BOTH SESSIONS (NORMAL SLEEP= NS; SLEEP DEPRIVED= SD; N=26)*

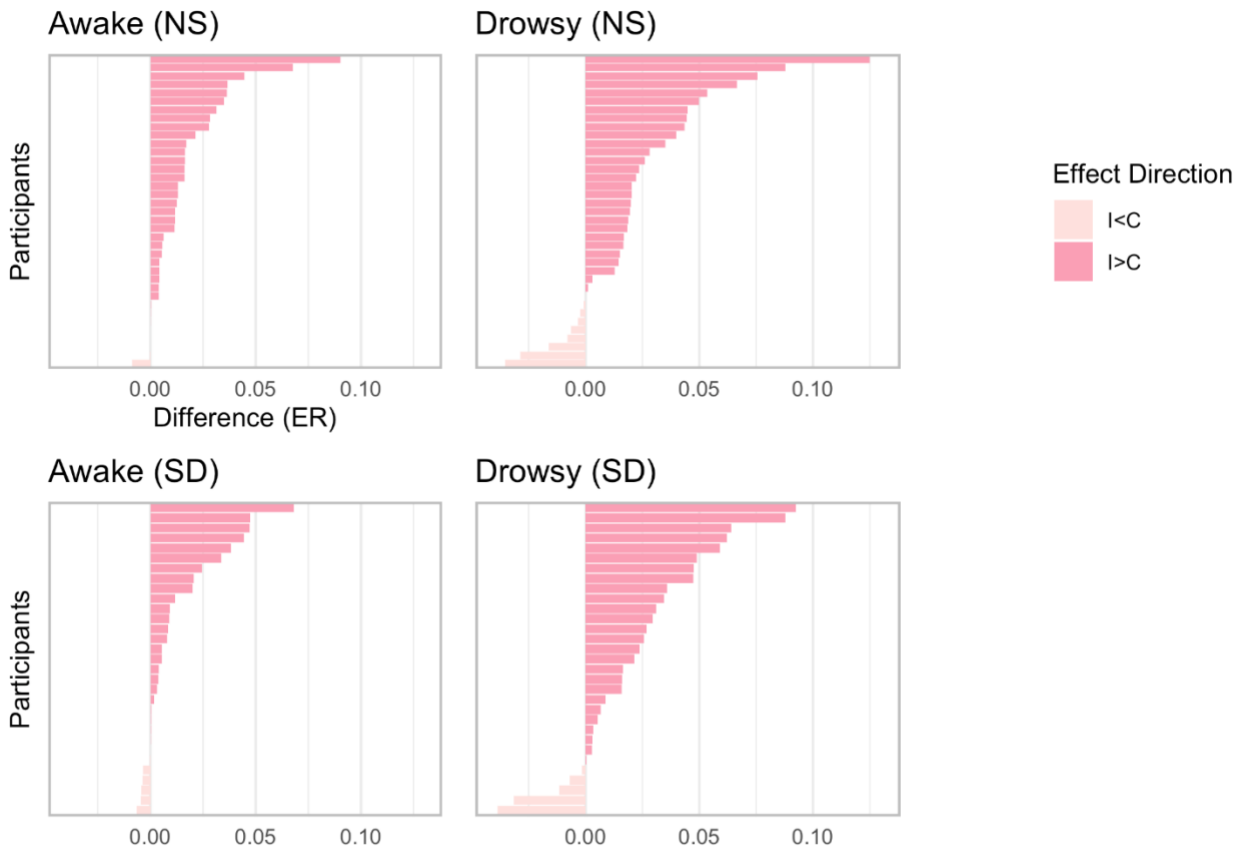

FIGURE 18. *INDIVIDUAL DIFFERENCES IN ERROR RATE (ER) ACROSS SLEEP AND ALERTNESS CONDITIONS FOR ALL PARTICIPANTS. NS: NORMAL SLEEP; SD: SLEEP DEPRIVED*

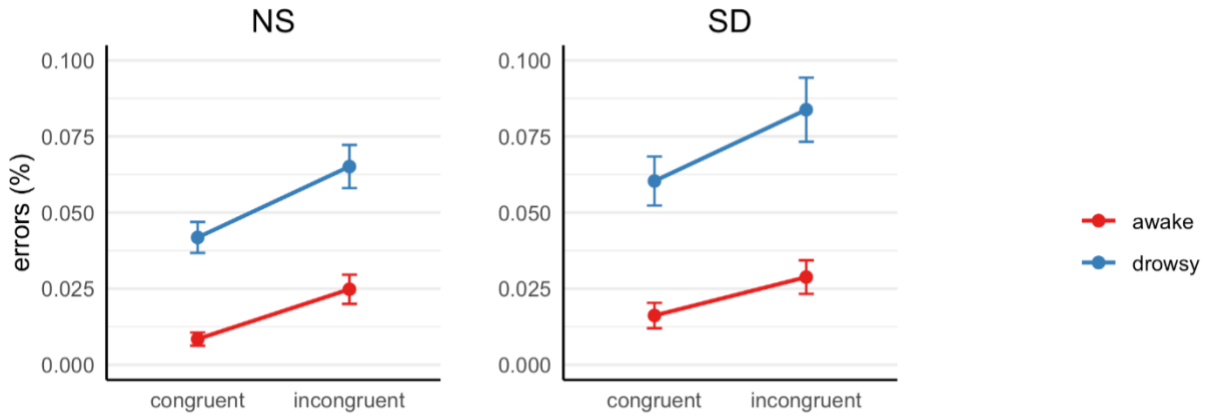

FIGURE 19. *MEAN ERROR RATES ACROSS PARTICIPANTS WHO ATTENDED THE NORMAL SLEEP (NS) AND THE SLEEP DEPRIVED (SD) SESSIONS (N=26)*

On the other hand, while individual mean differences seem to show a clear effect of conflict across conditions, a conflict adaptation effect appears to be more clearly present during wakefulness, regardless of whether participants were sleep deprived or had slept normally. Such a trend is not apparent in the drowsy trials of neither sleep condition.

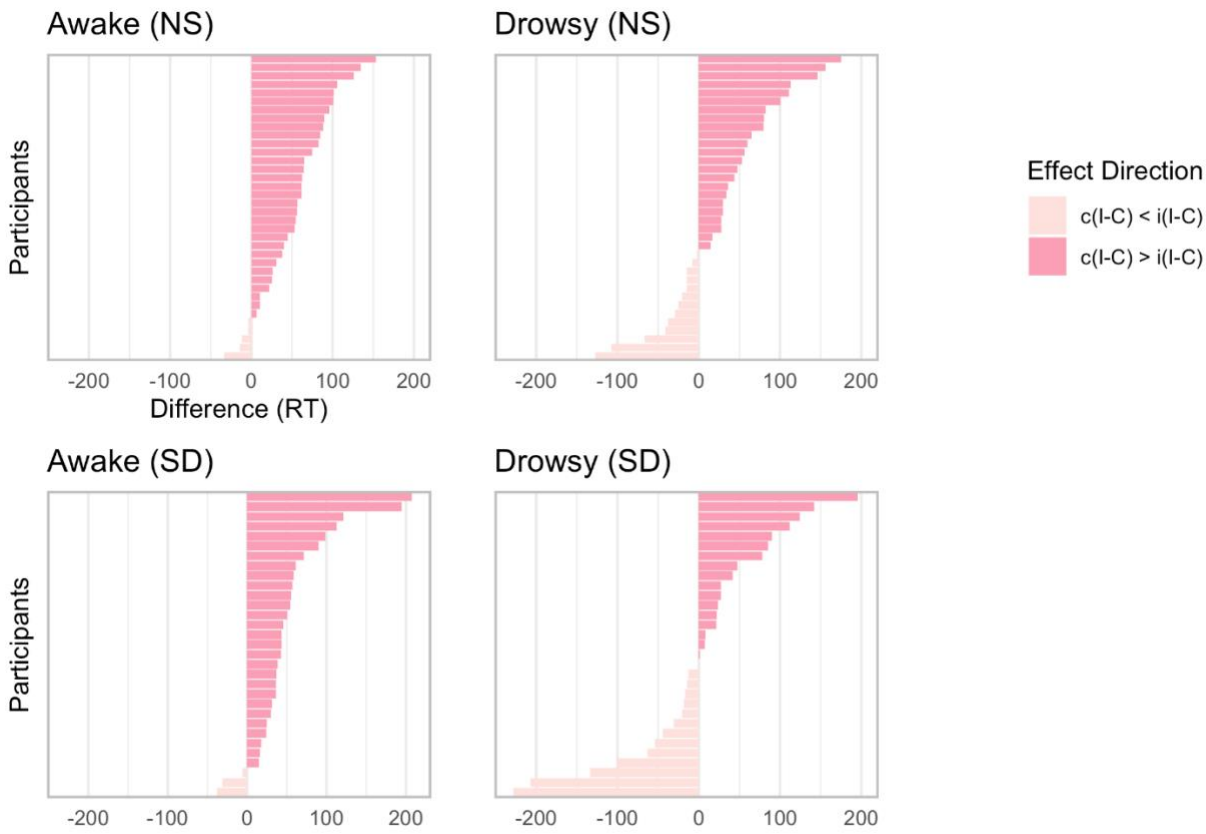

FIGURE 20. ADAPTATION EFFECT BY PARTICIPANT SHOWING INDIVIDUAL RT DIFFERENCES. ADAPTATION DIFFERENCES WERE COMPUTED AS (CI-CC)-(II-IC). A POSITIVE DIFFERENCE INDICATES A CONFLICT ADAPTATION EFFECT.

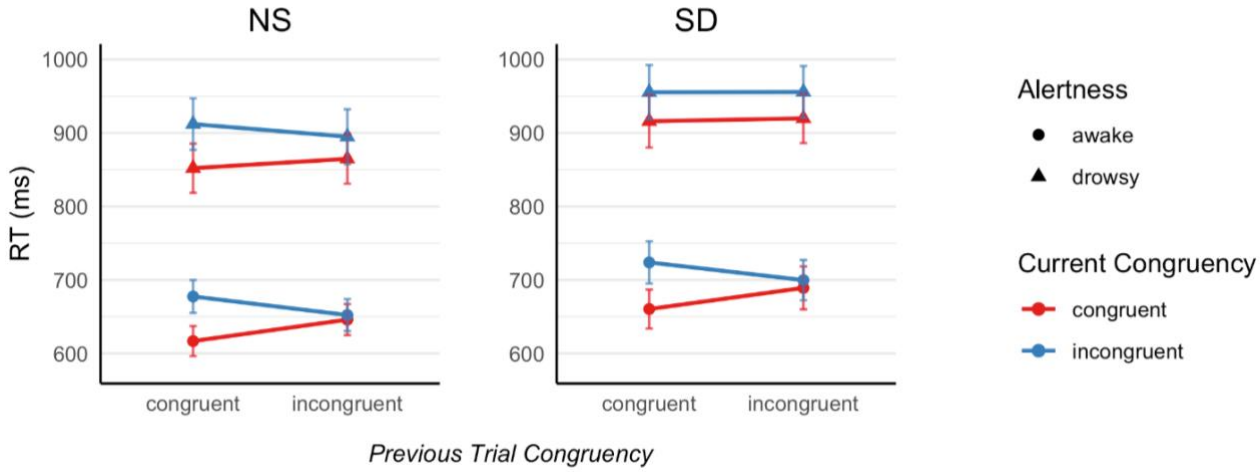

FIGURE 21. *CONFLICT ADAPTATION IN THE NORMAL SLEEP (NS) AND SLEEP DEPRIVED (SD) CONDITIONS. POINTS INDICATE GRAND MEAN. SEM BARS.*

4.5.2 Multilevel Modelling

A mixed effects model approach was chosen to analyse our RT data. Mixed effects models offer a main advantage for our design, namely, they allow for participants with missing data to be included in the analysis. Additionally, mixed effect models allow for different number of observations, meaning that we were able to use trial-by-trial information in our analysis, as opposed to RT means by participant that an rmANOVA would require.

As explained in the Methods section of this chapter, we began building our model by defining the random effects that best described our data. A random intercept by subject was assumed, however different random slopes were added and compared in a stepwise manner, as shown on Table 1. Ultimately, random intercept and random slope model was deemed to be the most optimal, using sleep, alertness and their interaction as random slope by subject.

TABLE 2. LRT FOR RANDOM EFFECTS SELECTION IN RT MODEL (N=42)

	Model Selection				
	First step				
Random Effects	**Model**	**df**	**Log-likelihood**	**χ2(df)**	***p*-value**
ID†	0	2	-15582		
+ Alertness‡	1	2	-13487	4189.7	***
+ Sleep‡	2	2	-14309	2545.5	***
+ Congruency‡	3	2	-	-	Does not converge
+ Previous congruency‡	4	2	-	-	Does not converge
	Second step				
Random Effects	**Model**	**df**	**Log-likelihood**	**χ2(df)**	***p*-value**
Alertness‡|ID†	1	2	-13487		
× Sleep‡	7	7	-11682	3610.3	***
+ Sleep‡	6	3	-12070	2832.7	***

†: Random intercepts

‡: Random slopes

χ2 = Pearson's Chi-squared test; df = degrees of freedom

*** significant at p <0.001

Upon establishing our random structure, we moved to determine the optimal structure for our fixed effects. Following Zuur, et al (2010), we used LRT to remove effects in a stepwise fashion. Starting from a maximal effects model (as opposed to building from the most simple model upward) has been suggested to be the most optimal for psychological data, as it yields more generalisable findings and ensures no loss of explanatory power by wrongly including information as a random effect (Barr et al., 2013; Zuur et al., 2010).

Table 2 shows our model selection process. Effects were removed in a stepwise fashion and each sub-model was compared to the full model in its respective step. Effects where no difference was observed upon removal were subsequently dropped in the following round. A final step is shown to indicate that removal of sleep from our fixed effects resulted in a significant difference, thus ending our model selection process.

TABLE 3 . LRT FOR SELECTION OF FIXED EFFECTS IN RT MODEL (N = 42)

	Model Selection				
	First step				
Fixed effect	**Model**	***df***	**Log-likelihood**	**χ^2 (*df*)**	***p value***
Full model 1	1		-11682		
- sleep:alert:prevcong:cong	1A	1	-11682	0.4386	0.5078
	Second step				
Full model 2	2		-11682		
- sleep:alert:prevcong	2A	1	-11682	0.2653	0.6065
- sleep:alert:cong	2B	1	-11682	1.2349	0.2665
- sleep:prevcong:cong	2C	1	-11683	2.083	0.1489
	Third step				
Full model 3	3		-11684		
- sleep:alert	3A	1	-11684	0.0001	0.9906
- sleep:prevcong	3B	1	-11684	0.2129	0.6445
- sleep:congruency	3C	1	-11684	0.0025	0.9604
	Fourth Step				
Full model 4	4		-11684		
sleep	4A	1	-11686	4.9394	*

χ^2 = Pearson's chi-squared test; Df = degrees of freedom

* significant at $p < 0.05$; *** significant at $p < 0.001$

Our final model was then established as follows:

⇒ **Fixed component:** sleep + alertness × previous congruency × congruency

⇒ **Radom slope:** sleep × alertness

⇒ **Random intercept:** ID

An inspection of our chosen model (type III ANOVA with Satterthwaite's Method) revealed main effects of sleep condition ($F_{(1,29)}$= 5.15, p=0.031), alertness ($F_{(1,41)}$= 84.05, p<0.001) and congruency ($F_{(1,56556)}$= 464.46, p<0.001). An effect of adaptation was also found, indicated by a significant interaction between previous and current trial congruency ($F_{(1,56560)=}$ 157.60, p<0.001). A significant interaction between alertness, previous congruency and current congruency was also observed ($F_{(1,56560)}$= 15.74, p<0.001).

No significant effect was observed for previous congruency ($F_{(1,56556)}$= 0.5027, p=0.478), nor was there a significant effect of the interaction between alertness and congruency ($F_{(1,56556)}$= 1.9035, p=0.17). To investigate this further, a post-hoc analysis was performed by contrasting two linear models on log-transformed RTs. Stimulus congruency and alertness were included into the fixed component for both models. Crucially, the interaction term from one of the models, as follows:

Interaction model

⇒ **Fixed component:** alertness + congruency + alertness:congruency

⇒ **Radom slope:** sleep × alertness

⇒ **Random intercept:** ID

Independent effects model

⇒ **Fixed component:** alertness + congruency

⇒ **Radom slope:** sleep × alertness

⇒ **Random intercept:** ID

TABLE 4. MODEL COMPARISON

Model	Fixed Parameters	Random Parameters	Log-Likelihood	Pr(>X^2)
Independent	Alertness + Congruency	Slope: sleep * alertness; Intercept: ID	-11776	
Interaction	Alertness * Congruency	Slope: sleep * alertness; Intercept: ID	-11774	0.1724

We used the 'anova' function on the lmerTest package from R (version 3.1-2) to compare different models' performance. As predicted, the Interaction model for RTs was no better than our Independent Effects model (table 3). As further validation, when we compared our independent effects model to a null model which contained only the mean as a fixed parameter, i.e. the simplest fixed parameter (not shown on table), the ANOVA revealed the independent effects model to be better than our null model ($X^2(2)= 512.578$, $p<2.2e-16$).

4.6 Discussion

On this chapter, we sought to investigate the effect of drowsiness and sleep deprivation on cognitive control, operationalised via the conflict effect. Our main hypothesis was simple. If conflict detection is a fast, unconscious process, but conflict adaptation is long-term and consciousness-dependent, we should see a dissociation of the two processes indicated by performance during drowsiness. By contrast, we expected sleep deprivation to impair conflict detection mechanisms during drowsiness, in addition to conflict adaptation.

Conflict detection was shown to be robust to all of our experimental manipulations, persisting throughout drowsiness even when participants were partially sleep deprived, counter to our hypothesis that sleep deprivation would impair conflict detection. This provides evidence that conflict detection is an automatic process robust to alertness and sleep manipulations. This is further illustrated by the low error rates exhibited across participants, indicating an all-or-

none process for conflict detection. I.e. as long as motor control can be executed, we can expect conflict detection to be reflected by behaviour.

Given that task-relevant language processing has also been shown to occur in reduced alertness and into N2 sleep (Blume et al., 2017; Kouider et al., 2014), we could consider making the task non-dependent on language by introducing other forms of mapping, for instance by using a tones rather than words as we did in our go/nogo paradigm. In this case, we might observe an effect of alertness on conflict detection, assuming a weaker audiomotor mapping to a tone compared to a word. It is important to keep in mind that detection of conflict is a downstream process that relies upon feature discrimination. In this case, those features are the physical location and semantic content of a sound, so we can indirectly infer that both of these processes are also present at reduced levels of alertness.

As evidenced by individual inspection of RTs, there is considerable between-subject variability in our data. A strength in our design was the high number of trials collected per condition, which we then used to model RTs in a way that more accurately accounts for between-subject variation, offering an advantage over rmANOVA. Indeed, an initial analysis of our behavioural data (Canales-Johnson et al., 2020) using a two-way ANOVA had suggested that conflict adaptation was unaffected by drowsiness. Yet through a mixed model we revealed an interaction between alertness, previous trial congruency and current trial congruency, suggesting that alertness modulates adaptation to conflict. This is in contrast to findings reported by (Van Gaal, et al., 2010), who found that a conflict adaptation effect was present even when conflict primes were masked. This suggests that alertness and awareness are not be functionally equivalent.

Importantly, we did not identify an interaction between alertness and congruency. Furthermore, a post-hoc analysis revealed no advantage of an interaction model over a simpler independent effects model, supporting our hypothesis that conflict detection is less reliant on consciousness, and thus can be

dissociated from the process of trial-by-trial conflict adaptation where reduced levels of alertness have a significant effect.

Interestingly, while our sleep deprivation condition had a general slowing down effect on RTs, no significant interactions emerged between sleep deprivation and our other explanatory variables. This might indicate that sleep deprivation does not modulate neither conflict detection nor conflict adaptation. However, it has also been suggested that log transformations of RT might obscure interaction effects. Therefore, null findings around interactions must be interpreted with caution.

A further limitation of our study was the lack of counterbalancing in the awake-drowsy order of sessions, which always consisted of the alert session first, followed by the drowsy session (figure 13). This was done in order to avoid a larger confounds of rest and napping. That is, if some sleep deprived participants had been allocated to the drowsy session first, there would have likely been an effect of nap/rest, conferring an advantage in performance over those who did not rest. Thus, alert sessions pre and post-drowsy would not have been equivalent. It is possible that not counterbalancing alert and drowsy sessions could have introduced practice effects into our analyses. However, previous studies have found practice effects during interference tasks (Davidson et al., 2003) to be modest at best in young adult samples.

5

Identifying the Neural Markers of Cognitive Control

In Chapter 4, I presented the behavioural results from 42 participants who performed an auditory Simon task whilst transitioning from wakefulness to sleep. This chapter is concerned with the EEG results of the same set of subjects. First, we performed a cluster permutation analysis on time frequency data to investigate the effect of conflict in the theta frequency band in the frontal-central electrodes. Midfrontal theta has consistently been reported in the literature as a neural marker of conflict, and more broadly cognitive control. We observed an expected cluster in theta associated to conflict during wakefulness, however, we did not find any the same differences during drowsiness. Similarly, we found a theta cluster in awake, sleep deprived participants, but not during drowsiness.

Following our univariate spectral analysis of EEG data, we used a multivariate decoding approach in order to investigate EEG patterns in our stimuli properties (i.e. location, semantic content, and congruency) without a priori selection of channels and allowing for greater flexibility across the time-frequency space.

5.1 Introduction

Cognitive control is an umbrella term, encompassing the range of mental processes that allow flexible, goal-directed behaviour. Such processes include impulse inhibition, error monitoring, task switching, and conflict detection, among others. Notwithstanding this diversity of functions, cognitive control has been consistently linked to prefrontal oscillatory activity in the EEG theta frequency band (Helfrich & Knight, 2016). Furthermore, frontal theta has been suggested by some to specifically reflect the detection of the need for control (Cavanagh & Frank, 2014).

The ubiquitous presence of theta across cognitive control tasks suggests it might be a robust neural marker, regardless of sensory dimension. Furthermore, Jiang and colleagues (2015) have found evidence that such a marker persisted even when conflict was unconsciously presented in a visual masking paradigm. Upon identifying that a behavioural conflict effect is still present during drowsiness both after a night of normal sleep and after sleep deprivation, we proceeded to investigate whether theta modulations associated with conflict would follow suit.

5.2 Research Questions

Considering that theta conflict effect generalises across tasks, even when conflict is not consciously perceived, this study investigates whether changes in theta power can still be detected in reduced states of alertness. Specifically, we were interested in the following questions:

1. Can we detect a theta marker of conflict during an auditory Simon task? As has been widely reported in the literature, we expected to observe an increase in theta power to associated to incongruent trials, compared to congruent trials. Even though most studies of conflict have been conducted in the visual domain, we expect the same theta marker to be associated with conflict in the auditory domain.

2. Is conflict-related theta modulated by changes in alertness? We expected the difference in theta power between congruent and incongruent trials to be reduced during drowsiness, as reflected by an interaction between drowsiness and congruency.
3. Does partial sleep deprivation modulate theta power during conflict detection? Similarly to drowsiness, we expected sleep deprivation to have a modulatory effect on theta during conflict.
4. If so, at what level of processing is the conflict effect modulated by changes in alertness? In order to better understand the cognitive dynamics of the conflict effect, we used multivariate spectral decoding to classify stimulus congruency alongside location and semantic content of the stimuli. We expected that if reduced alertness is selectively targeting cognitive control, we should expect stimulus properties continue to be represented during drowsiness even in cases when congruency is no longer classified above chance.
5. Are conflict-related power differences related modulated by previous trial congruency? We expected the conflict adaptation effect observed in behaviour to be reflected by an interaction between previous trial congruency and current trial congruency.
6. Is the effect of alertness on conflict adaptation mirrored by a similar effect on time-frequency power differences? We expected alertness to modulate differences in conflict-related theta reflecting the effects observed during conflict adaptation described in the previous chapter. Therefore, an interaction between alertness, previous trial congruency, and current trial congruency was expected.

5.3 Methods

5.3.1 Behavioural paradigm

For a detailed description of our behavioural paradigm, see Chapter 4.

5.3.2 Participants

See section 4.4.1 for information on participants. Note that, except for when individual data is shown, all analyses were performed on the subset of participants who attended *both* the normal sleep and the sleep deprived sessions (n=25).

5.3.3 EEG Analysis

Approximately two hours of 128-channel high-density EEG data were collected for each participant with EGI electrolyte caps (Electrical Geodesics Inc., Oregon, USA), divided over separate datasets for the awake and drowsy part of the experiment. Data were recorded in microvolts (μV), sampled at 500 Hz and referenced to the vertex, using the Net Amps 300 amplifier (Electrical Geodesics Inc., Oregon, USA).

Pre-processing was done by means of custom-made MATLAB (R2016, The MathWorks, Inc.) scripts supported by EEGLAB (Delorme & Makeig, 2004). Data form 92 channels over the scalp surface were retained for further analysis. Channels on the neck, cheeks and forehead, which are thought to contribute more movement-related noise than signal (Chennu et al., 2014), were excluded. Continuous EEG data were first down-sampled to 250 Hz, filtered between 0.5 – 40 Hz and segmented into epochs from -1.5 to 2 s around stimulus onset. Thus, given that the minimal inter trial interval was 2 seconds, the pre-stimulus period of epoch *n* could overlap maximally 1.5 seconds with the post stimulus period of epoch *n-1*.

Individual trials were then classified into awake and drowsy trials using the method described in Canales-Johnson, et al (2020; chapter 4). In contrast to the -4s

pre-trial segments originally used in Jagannathan, et al (2018), we used a -1.5s to 0s window to avoid trial overlap. RT variability and visual inspection of changes in power between awake- and drowsy-classified trials partially validated this approach. A typing error in Canales-Johnson, et al (2020) omitted theta from the frequency bands used in the coherence analysis of microstage classification, but it was in fact included.

Subsequently, channels with a variance of 500 or higher were rejected. Independent Components Analysis (ICA) based on the Infomax ICA algorithm (Bell & Sejnowski, 1995) was done over all remaining channels. The topography and time course of the 20 components accounting for most variance in each dataset were inspected. Components typical of saccades and muscle artefacts were removed from the EEG signal (Delorme & Makeig, 2004). Eye blink artifacts were identified by highly localised anterior distribution of weights, with sparse, large amplitude peaks across trials. Similarly, saccade components were highly localised to frontal channels, with a distinctive dipole pattern reflective of eye movements from side to side. Muscle artifacts were identified as localised, high frequency bursts with a power spectrum activity largely distributed towards higher frequencies. A conservative approach was adopted, with a range of 3-6 components rejected per dataset.

After component rejection, the signals from the previously rejected channels were replaced with the average activity in all remaining channels by spherical spline interpolation. Trials were then rejected if they exceeded certain thresholds for amplitude (below -1500 microvolts or above 1500 microvolts) or slope (above 60 microvolts). Finally, data were re-referenced to the average of all channels.

The first trial of each block was discarded. Missed trials and incorrect trials were also removed from analysis, as well as trials with RT <200ms. For the conflict adaptation analyses, we included only trials where both previous trial and the current trial were correct.

5.3.4 Time Frequency Analysis

Epochs were grouped according to trial congruency. EEG traces were then be decomposed into time-frequency charts ranging from 2-30 Hz in 15 linearly spaced steps of 2 Hz per bin. We then obtained the power spectrum of the EEG signal via the fast Fourier transform, and then multiplied that by the power spectra of complex Morlet wavelets with logarithmically spaced cycle sizes ranging from 3 to 12. Using the inverse Fourier transform, we then obtained the complex signal, which was then converted to frequency-band specific power by squaring the result of the convolution of the complex and real parts of the signal. The resulting time-frequency data was then averaged per subject and trial type. The resulting time-frequency traces were then transformed into decibels and normalised to a baseline of 400ms to -100ms before stimulus onset. The above analysis was carried out in a fronto-central region of interest (ROI) defined by the hypothesis that conflict is indexed by a rise in mid-frontal theta power (for electrode positions see figure 23). In order to define the ROI for , we reduced the number of electrodes to four, given that the cluster reported in Canales-Johnson, et al (2020) was not observed under the original 5 electrodes. This subset of 4 electrodes was used in all subsequent analyses.

In order to derive a time frequency region of interest (tf-ROI), we computed the overall conflict difference (i.e. incongruent-congruent) regardless of alertness or sleep deprivation condition, with epochs averaged per subject in each pairwise comparison. We used the method described by Maris & Oostenveld (2007), comparing subject-wise averages at corresponding time points in one-tailed dependent (for within-subject comparisons) or independent (for between-subject comparisons) sample t-tests. Adjacent temporal points whose p-values were<0.05, were clustered together by summating their t-values. Using the Monte Carlo method, this process of random partitioning and clustering was performed for 1000 iterations. The time-frequency cluster with largest t-value was retained each time, constructing a histogram of multiple test statistics which was then used to determine

clustering threshold. A nonparametric estimate of the p-value on the resulting cluster was then obtained (Cohen, 2014).

Following this step, we investigated differences between our conditions by extracting the time-frequency power averages from within the previously defined cluster. These were then analysed using a rmANOVA that contained sleep, alertness, and congruency as levels. A separate rmANOVA was performed to test for adaptation (i.e. interaction effects between current and previous congruency) given that we wanted to avoid the bottleneck effect on trial number that inherently arises from pairing trials together.

5.3.5 Multivariate Spectral Decoding

Recently, multivariate spectral decoding has become widely used to investigate differentiation between cognitive processes in the brain. In other words, is the information between conditions different enough to be accurately decoded by the classifier?

The multivariate approach has been shown to be more specific than univariate methods such as the power analysis described previously (Fahrenfort et al., 2017), and thus might be better suited to answer general questions about stimulus representation across different levels of alertness.

We used the ADAM toolbox (Fahrenfort, et al. 2018) on raw EEG data split by alertness level, which was transformed to time-frequency using the default methods with similar epoch lengths (-200ms to 1200ms, 2Hz to 30Hz). Trials were further split according to sound location (left-presented vs right-presented), semantic content ("left" vs "right") and congruency (congruent vs incongruent). Given the lengthy time periods associated to decoding algorithms, data were downsampled to 64Hz. Time-frequency data from all scalp electrodes were then fed to a backward decoding algorithm, with either sound location, semantic content or

congruency as stimulus class, applied according to a 10-fold cross-validation scheme. A linear discriminant analysis (LDA) was used to discriminate between our stimulus classes and classification accuracy was determined by measuring the area under the curve (AUC), as defined by signal detection theory. The AUC scores were compared across participants at each timepoint with double sided t-tests against a 50% chance level. A cluster based permutation test ($p<0.05$, 1000 iterations) was used to control for multiple comparisons, yielding clusters with significant above-chance classifier accuracy.

5.4 Results

5.4.1 Univariate analysis revealed a positive theta cluster associated to conflict

Upon finding that conflict detection is not modulated by alertness, we expected to find the increase in oscillatory power in mid-frontal (MF) theta (4-8Hz) associated to conflict, thus providing further evidence for MF theta as a ubiquitous marker of cognitive control in line with previous findings from Jiang and colleagues (2015). Indeed, we observed the expected theta cluster ($p=0.045$, frequency range: 3-17Hz, time-range:260-820ms) when collapsing trials within subject across conditions of alertness and sleep (figure 22).

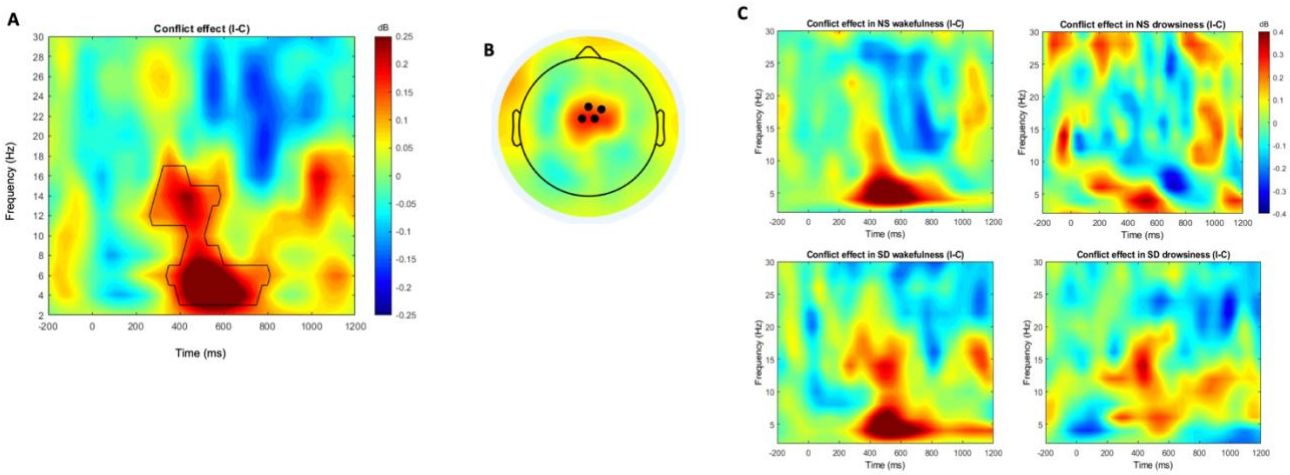

FIGURE 22. CONFLICT EFFECT MEASURED AS INCONGRUENT MINUS CONGRUENT (I-C) DIFFERENCES IN DB TRANSFORMED POWER. (A) TF-ROI CLUSTER IDENTIFYING DIFFERENCES IN POWER ASSOCIATED WITH CONFLICT. (B) TOPOGRAPHIC SCALP MAP INDICATING ELECTRODE POSITION. (C) TF CHARTS SHOWCASING I-C DIFFERNCES IN EACH CONDITION.

The area around the cluster described above was then used as our time frequency region of interest (TF-ROI) to enter into an rmANOVA, which revealed a main effect of alertness ($F_{(1,24)}$= 3.75; p=0.050, η_p^2 = 0.151) –albeit marginally significant— and congruency ($F_{(1,24)}$= 47.10; p<0.001, η_p^2 = 0.662), as well as an interaction between alertness and congruency ($F_{(1,24)}$= 9.24; p=0.006, η_p^2 = 0.278). We did not observe a main effect of previous night sleep ($F_{(1,24)}$= 9.258e-5; p<0.986, η_p^2 = 1.344e-5). We also did not observe a significant sleep*alertness interaction ($F_{(1,24)}$= 0.045; p<0.664, η_p^2 = 0.008), nor an interaction between sleep and congruency ($F_{(1,24)}$= 0.057; p<0.442, η_p^2 = 0.027). A post-hoc Tukey test revealed differences only in the awake state for both the normal sleep ($t_{(24)}$=-3.49; p=0.018) and the sleep deprived ($t_{(24)}$=-3.75 p=0.008) conditions.

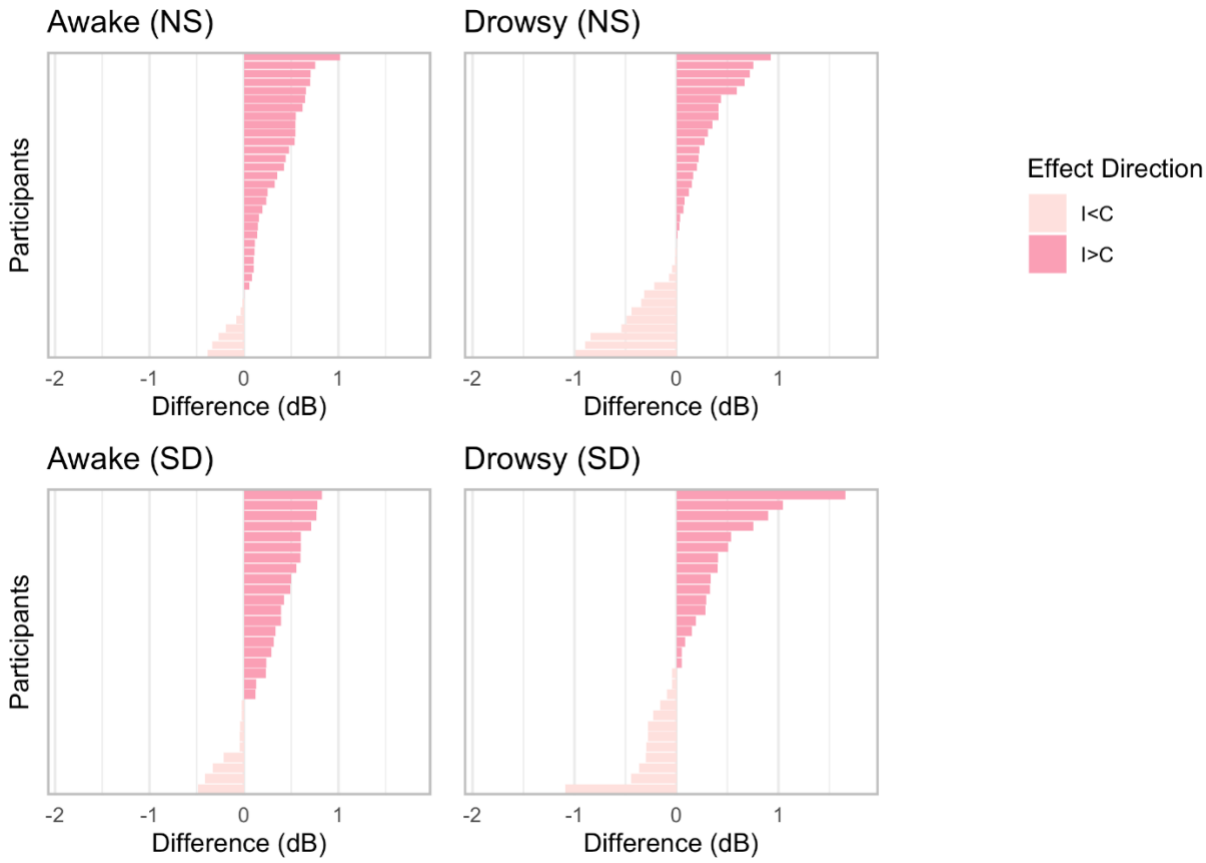

FIGURE 23. ***INDIVIDUAL DIFFERENCES IN POWER ASSOCIATED TO CONFLICT.*** **MEANS FROM THE TF-ROI WERE AVERAGED ACROSS TRIALS FOR EACH PARTICIPANT. POWER (DB) MEANS IN THE CONGRUENT TRIALS WERE SUBTRACTED FROM INCONGRUENT TRIALS (I-C). A POSITIVE DIFFERENCE INDICATES A CONFLICT EFFECT.**

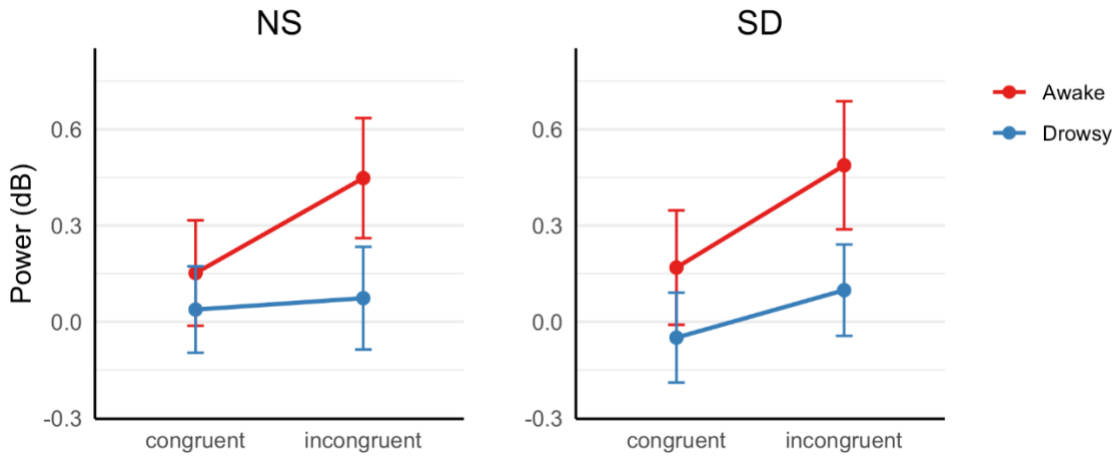

FIGURE 24. *THETA POWER AVERAGE ACROSS SUBJECTS DERIVED FROM WITHIN TF-ROI. BARS SHOW SEM.*

5.4.2 Conflict Adaptation

A subsequent rmANOVA revealed an interaction of previous congruency and current congruency ($F_{(1,24)}$= 10.173; p=0.004, η_p^2 = 0.298), indicating the presence of conflict adaptation. However, we did not find a significant interaction between alertness, previous trial congruency and current trial congruency ($F_{(1,24)}$= 0.006; p=0.897, η_p^2 = 7.155e-4). This might suggest that even though a conflict adaptation effect was not observed at the level of behaviour during drowsiness, it might still be present at the neural level.

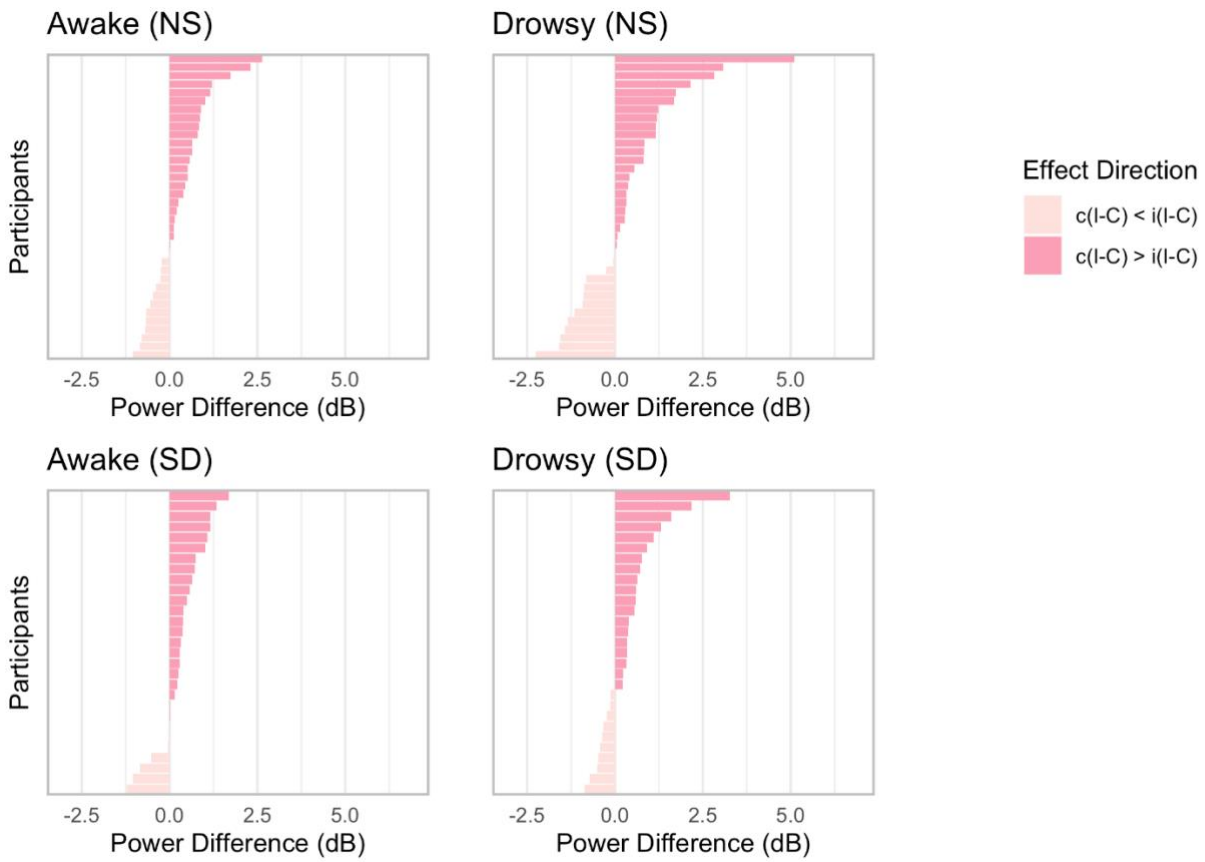

FIGURE 25. ADAPTATION EFFECT BY PARTICIPANT SHOWING INDIVIDUAL POWER DIFFERENCES IN THE TF-ROI. ADAPTATION DIFFERENCES WERE COMPUTED BY (CI-CC)-(II-IC). A POSITIVE DIFFERENCE INDICATES A CONFLICT ADAPTATION EFFECT.

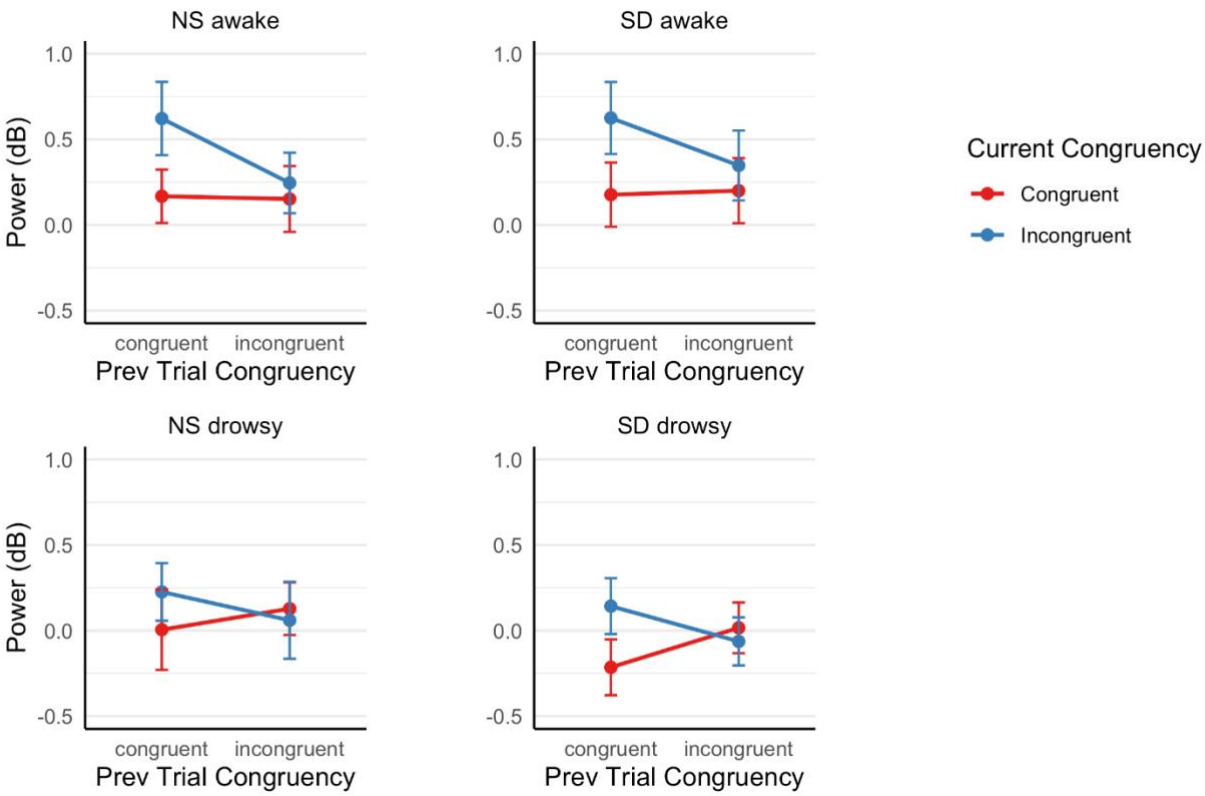

FIGURE 26. *POWER DIFFERENCES SHOWING CONFLICT ADAPTATION INTERACTIONS FOR DURING NORMAL SLEEP (NS) AND SLEEP DEPRIVATION (SD). POINTS INDICATE GRAND MEAN. SEM BARS.*

5.4.3 Multivariate Spectral Decoding

Given that a theta conflict effect was found to be unreliable during drowsiness, we reasoned that this could be due to reduced specificity in our univariate analysis. We therefore adopted a multivariate analysis approach using the ADAM decoding toolbox (Fahrenfort, et al., 2018) which enabled us to test for stimuli category representations without having to define our channels, frequency range, or time windows a priori. It would not be surprising that a more widespread pattern of neural activity in time and space might underlie the conflict effect during drowsiness.

In order to test for neural activation differences between our stimulus categories, we trained classifiers to distinguish stimuli properties from the EEG signal along 3 dimensions: location (i.e. left-presented vs right-presented), semantic content (i.e. "right" vs "left" meaning) and congruency (i.e. congruent vs incongruent). Above-chance classifier accuracy would imply neural processing of that dimension of the stimulus (Hebert and Baker, 2018).

We identified clusters with above chance classifier accuracy across conditions when it came to location and semantic features (figure 27). However, stimulus congruency was only decodable from the EEG signal in normal sleep wakefulness.

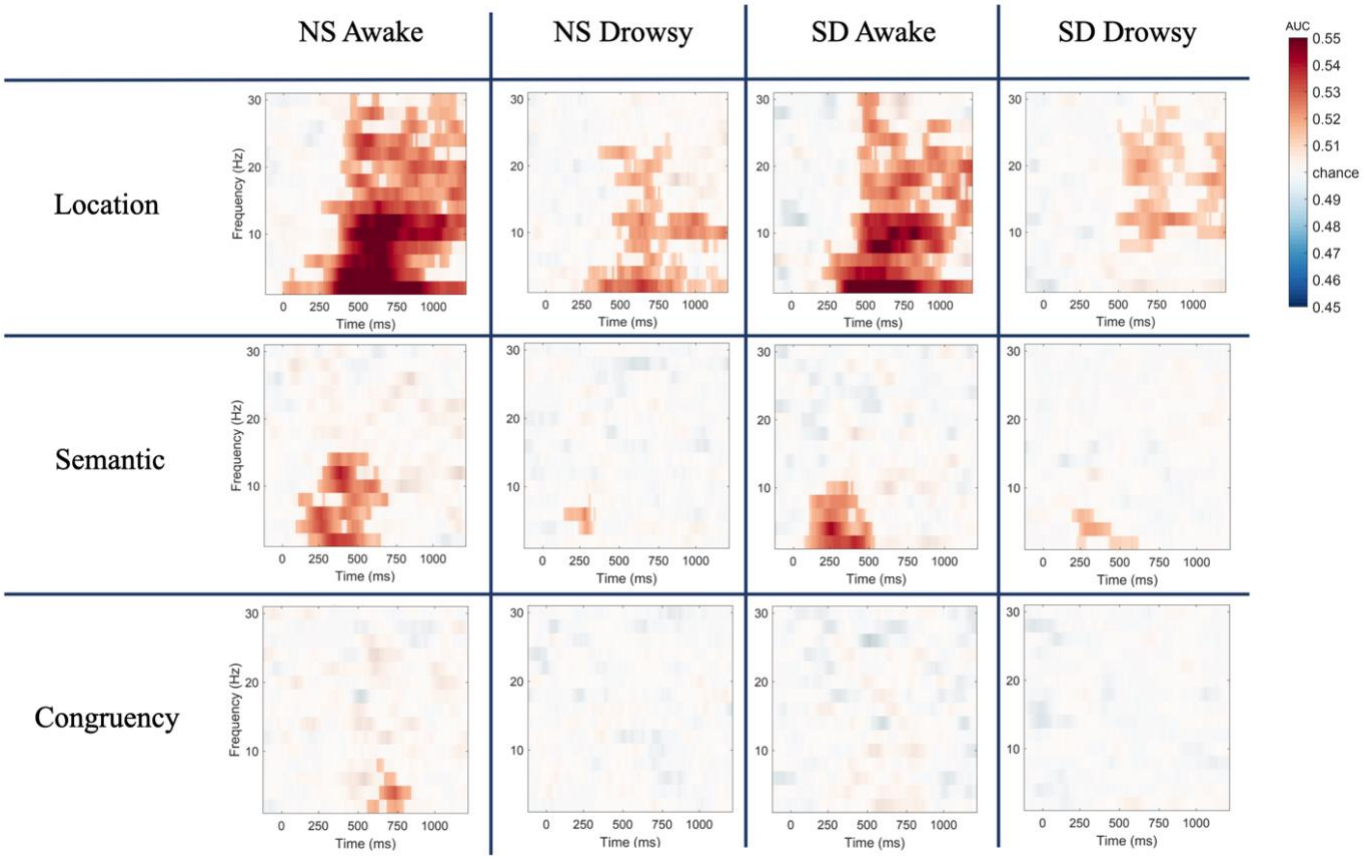

FIGURE 27. CLASSIFIER ACCURACY ACROSS ALERTNESS AND SLEEP CONDITIONS ARE SHOWN FOR DIFFERENT STIMULUS FEATURES. CLASSIFIER ACCURACY WAS THRESHOLDED THROUGH A CLUSTER-BASED CORRECTION ($P<0.05$) AND SIGNIFICANT AUC CLUSTERS ARE SHOWN WITH INCREASED CONTRAST. SEMANTIC AND LOCATION INFORMATION COULD BE DECODED IN ALL CONDITIONS. BY CONTRAST, CONGRUENCY WAS ONLY DECODABLE DURING WAKEFULNESS AFTER NORMAL SLEEP, BUT NOT DURING DROWSINESS EITHER AFTER NORMAL SLEEP NOR SLEEP DEPRIVATION. CONGRUENCY WAS ALSO NOT DECODABLE DURING WAKEFULNESS AFTER SLEEP DEPRIVATION.

TABLE 5. INDIVIDUAL STATISTICS FOR EACH CLUSTER IN THE MVPA ANALYSIS

Stim Category	Condition	Time Range	Peak Time	Freq Range	Peak Freq	*p*
Location	NS awake	4-1200	564	2-30	2	<0.001
	NS drowsy	260-1200	644	2-24	2	<0.001
	SD awake	212-1200	580	2-30	2	<0.001
	SD drowsy	484-1200	852	2-30	12	<0.001
Semantic	NS awake	100-692	388	2-14	12	<0.001
	NS drowsy	148-340	276	4-8	6	0.018
	SD awake	84-532	260	2-10	4	<0.001
	SD drowsy	196-612	324	2-6	4	0.005
Congruency	NS awake	564-835	740	2-8	4	0.024
	NS drowsy	-	-	-	-	-
	SD awake	-	-	-	-	-
	SD drowsy	-	-	-	-	-

5.5 Discussion

5.5.1 Univariate time-frequency analysis

In this chapter, we present results from a cognitive control study that employed a Simon task to investigate the effect of drowsiness and sleep deprivation on the neural signatures of conflict. Confirming our initial hypothesis and reports in the literature (Cohen & Donner, 2013; Helfrich & Knight, 2016; van Gaal et al., 2012), we were able to identify an MF theta signature associated with conflict during wakefulness along with a wider range of frequencies. Existing studies linking theta to the conflict effect in the auditory domain are scarce. Therefore, this finding

provides further evidence of theta as a robust marker of cognitive control, regardless of sensory modality.

Nonetheless, this marker was less reliable during drowsiness, likely reflective of wider neural changes that occur as a result of reduced alertness. It is also possible that the increased variability in behavior associated to drowsiness also increases variability in the neural signal through temporal smearing. Furthermore, null results from our ANOVA should be taken with caution. It is possible that a different statistical method such as mixed modelling might have yielded different results by incorporating individual differences in theta variance associated to conflict.

After assessing univariate differences in the conflict effect, we used a MVPA classifier in an attempt to shed light on patterns of neural activity resulting from non-linear changes associated with reduced alertness. We also attempted to further probe the depth of information processing of different stimulus dimensions across alertness levels.

5.5.2 Multivariate spectral decoding

In order to better characterise the cognitive fragmentation that comes with the descent into sleep, we trained classifiers to differentiate our stimuli across different dimensions using the raw EEG signal. This was intended to identify the level at which the loss of conflict-related neural markers was occurring. Interestingly, we found that the single stimulus features relevant for conflict detection (i.e. stimulus location and semantic content) were decodable from the EEG signal during alertness and –crucially— during drowsiness. However, requiring an integration of the two dimensions, congruency was only decodable during wakefulness in the normal sleep condition. Whilst we did not test this hypothesis directly, we cannot rule out that the difference we observe in decodability of congruency might be a downstream result information processes related to lower level processing of location and semantic information.

The finding that the conflict effect still behaviourally present but not detectable through our univariate or multivariate approaches suggests the possibility for secondary process that is responsible for the detection of bottom-up conflict which might not be available in the frequency data. Indeed, we found that conflict is associated with a reconfiguration of wider network theta connectivity which is only predictive of RT differences during drowsiness (Canales-Johnson et al., 2020).

Gel electrodes are routinely used in overnight experiments, with duration in the order of 7-8 hours. The manufacturer manual for the EGI 128-eletrode Geodesic Sensor Net advises continuous usage for up to 12 hours. Therefore, it is unlikely that any of our findings are the result of any changes in impedance. Furthermore, electrode impedances were always checked in between the awake and drowsy sessions to ensure that they remained below 100 kΩ. For a discussion on practice confounds, please see the discussion in chapter 4.

6
Discussion

The world is an unpredictable place. Yet we seldom take any notice of the unexpected circumstances that we navigate through every day, from the pothole on the pavement we narrowly avoid, to the effortless turning of a frown into a smile when we run into a friend. The complex neural system that enables such behaviours is constantly operating outside our awareness, leading some to argue that conscious experience is merely the by-product of information processing in the brain.

However implausible, the theory that consciousness has no function is difficult to test empirically. Yet it is possible to track cognitive changes as we transition from a conscious state (wakefulness) into an unconscious state (sleep) in the hopes that it reveals the cognitive functions that are most likely to be dependent on consciousness. This thesis asks the question: to what extent are processes of cognitive control modulated by alertness?

6.1 Key findings

This thesis set out to investigate the mechanisms that underlie cognitive control in the transition from wakefulness to sleep. We have identified that reductions in alertness are generally associated with slower reaction times, increased error rates and higher unresponsiveness. However, these key features of drowsiness are manifested differently depending on the cognitive task to be performed.

In Chapter 2, we found that processes involving conflict monitoring are particularly impaired during drowsiness, suggesting of a specific effect of alertness on cognitive control. This was further supported by our finding that responsiveness decreases as a function of alertness. Together, these findings suggest that cognitive control is more susceptible than lexical decision making to the transition from wakefulness to sleep.

Similarly, we revealed an effect of drowsiness on conflict adaptation but not conflict detection, further suggesting that alertness has a detrimental effect when information must be integrated across time at a global neural scale. Our neural findings suggest an emergence of an alternative mechanism that is not reflected on theta activity in midfrontal electrodes, but rather a wider theta connectivity increase.

6.2 Alertness, responsiveness and sleep

For a long time in the psychological sciences, "consciousness" was a taboo word, too difficult to operationalise and judged to be outside of reach to the scientific method. In 2003, Baars wrote: 'psychologists avoided consciousness for most of the twentieth century. The central topic in psychological science became taboo. Those with serious interest in it risked professional suicide.' (p. 4)

However, while some of the criticisms levelled against the study of consciousness remain to this day (remember the hard problem), enormous progress has been made in the last 4 decades, and the field of consciousness science is now thriving. This is more likely due to conceptual progress than technological advancements, as some of the most widely used brain recording methods in cognitive neuroscience were invented decades (MEG, fMRI), or even centuries ago (EEG).

In the context of disorders of consciousness (DOC), Bekinschtein, et al. (2009) argued that disambiguating between alertness and responsiveness was necessary to fully characterise the spectrum of DOC's and beyond. Under this framework, responsiveness refers to "the capacity of the system to respond", while sensory alertness is defined as the degree to which sensory stimuli can affect the system, *regardless* of response. For the purpose of this thesis I would add that alertness can be conceived as a linear dimension, decreasing gradually as we transition from wakefulness to sleep. Notably, this definition is dissociable from conscious state. For instance, a dreaming person considered to be conscious, might be less alert than someone in dreamless N2 sleep.

Defining alertness in such a way has a clear advantage from an information processing point of view: once we know sensory processing *has* occurred, we can ask *what* sensory processing has occurred at different levels of alertness, thus being able to more accurately track the neurocognitive signatures of the sleep onset period. Using this linear dimension, wakefulness and drowsiness can be thought of as two different points in the alertness spectrum.

Under the proposed framework, alertness is also dissociable from arousal. Although both concepts are dependent on each other, alertness corresponds to the the baseline capacity of the cognitive system to be perturbed by sensory input, while arousal refers to the physiological/cognitive state once the system has already been perturbed, either by an external stimulus or intrinsic fluctuations. For instance, a

microarousal is typically short perturbation that happens during a period of low alertness, i.e. sleep. Similarly, sleep deprivation can be conceived of a state that is largely associated with low arousal and homeostatic pressure towards reduced alertness.

6.3 Effects of alertness on cognitive processing

After a long series of studies conducted in our lab and others (e.g. Bekinschtein, et al., 2009, Canales-Johnson, et al., 2020; Jagannathan, et al., 2018; Kouider, et al., 2011; Noreika, et al. 2015), we have learned to expect some consistent findings:

1) Alertness fluctuates rapidly: Participants tend fluctuate in alertness even during short 5-7min blocks. Such fluctuations can vary on a trial by trial basis, and are highly variable between subject and task.

2) RTs slow down and spread out: reaction times become slower and more variable during reduces levels of alertness. This is fairly constant among participants.

3) Errors increase with drowsiness: as participants become drowsy, the proportion of errors increases.

4) Lack of responsiveness: despite the usual increase in error rate, is noteworthy that rather than subjects performance becoming progressively worse up to the point of unresponsiveness, they seem to stop responding altogether. For example, errors in our conflict study did not go above 1% even during drowsy blocks containing a large number of unresponsive trials.

5) Semantic information processing continues well into N1 and early N2: as shown in this thesis and by Canales-Johnson, et al. (2020), people continue to execute motor commands during N1 (Canales-Johnson, et al., 2020), and semantic categorisation persists even after loss of motor response in N2 (Kouider, et al., 2015).

Lack of responsiveness might be adaptive, in order to avoid behaviours that might put an individual in danger. I.e. before behaviour becomes uncontrolled, the motor system shuts down to avoid negative outcomes. We have sought to expand the characterisation of the SOP, as proposed by Ogilvie (2001), and in turn obtain a clearer understanding regarding the function(s) of consciousness.

This thesis attempts to elucidate a further key point in the understanding of the effects of consciousness on cognition:

> 6) Alertness differentially affects cognitive processes: the general lesson from this thesis is that whilst reductions in alertness generally affect cognitive efficiency (i.e. by making them slower), it does not affect all processes equally. Furthermore the interactions between process and level of alertness can be used to determine the functional role of alert wakefulness.

6.4 Alertness and conflict monitoring

Our results from Chapter 2 revealed that conflict monitoring is specifically affected by modulations in alertness when compared to simpler perceptual decision processes. What is it about reduced alertness that might preserve one process better than the other? Even though 'Go' trials in both tasks were physically equivalent (i.e. same tones, duration, and ISI) interpreting what goes on before the button press is not straightforward.

Interestingly, we did not observe any differences between tasks in awake or even mild drowsy levels, yet the fact that we observed differences in drowsiness might seem to suggest alternative explanations. For instance, it is possible that the decision to go left or go right gets delayed, and so when the time comes to make a second Go/NoGo decision, it needs to "wait" for the first decision to be made. However, we argue that this is unlikely to be the case, given that responses in the simple Go task were not found to be slower during reduced alertness. If anything

there was a small trend toward faster responses (most likely a chance event). This indicated that decisions to go left or go right gets made early during the ISI and therefore our effect is likely not due to a processing bottleneck.

Another possible interpretation for our finding could be that the representation of the motor plan in WM is interfering with the conflict monitoring process, indicating that what we are seeing is indeed an interaction between WM and conflict monitoring mediated by alertness, rather than a simpler interaction between alertness and conflict monitoring. Whiles this possibility is harder to rule out, it is likely that the motor plan becomes locked as soon as the decision is made and therefore does not interfere with the subsequent performance of the task. A simple way to rule out this hypothesis would be to make the response criteria even simpler by having only one option for response (one button with left and right hand counterbalanced between blocks) and just having a warning cue indicating the upcoming Go/NoGo cue. Finding a similar effect when comparing this task to the Go task would provide further evidence that the effect is driven by impaired conflict monitoring.

6.5 Alertness and spatial attention

At their core, most integration frameworks suggest that sensory information is initially processed in primary sensory cortices, and stimulus features become progressively integrated through a bottom-up processes in other cortical areas. Thus, higher order stimulus features are reliant on successful processing of information at the bottom. Following this reasoning, detection of conflict in our auditory Simon task is reliant on at least 3 cognitive events:

1. Successful processing of location
2. Successful processing of semantic information
3. Successful integration of location and semantic information

Our findings add to previous studies that suggest all these three processes are somewhat preserved as we enter N1 sleep, and possibly early N2 (e.g. Bareham, et al., 2014; Kouider, et al., 2015). However, it is possible to imagine scenarios where each of the processes listed above fails in turn. For instance, an early impairment in location processing could potentially result in improved performance, as task irrelevant information would not cause interference. Indeed, we found indications that the conflict effect during drowsiness might be driven by stimuli presented on the left side (Wang, 2018), who reported an interaction effect between congruency and stimulus location on RT and error rates.

This is in line with previous studies from our lab which reported a rightward shift in attention during the SOP (Bareham, et al., 2014). Specifically, Bareham et al. (2014) found that stimuli presented on the left side were more likely to be misattributed to the right side, but only in drowsy trials (Hori stages 4-7). In the context of our conflict effect, we interpret this phenomenon would result in reduced right-sided incongruence, meaning that left-sided "right" stimuli would interfere less, as they would be misattributed as occurring on the right side. On the other hand, right-sided "left" stimuli would continue to interfere as the spatial location on this side of space can still be judged accurately.

Despite the theta power interaction between alertness and congruency, it is clear that spatial attention is preserved enough that location information still interferes with semantic information, as reflected by RTs and error rates. Furthermore, our MVPA results directly confirm that location information is still processed during drowsiness.

6.6 Semantic processing during sleep and drowsiness

Sleep has often been defined as a behaviour (e.g. Ogilvie, 2001). In a view first articulated by Flanigan (1973), sleep was conceived purely on behavioural terms as long as it met 4 criteria: (a) stereotypic or species-specific posture; (b) behavioural

quiescence; (c) elevated behavioural threshold; and (d) rapid state reversibility with relatively intense stimulation.

However, this leaves the SOP in a theoretical limbo, where it neither meets the criteria for sleep, nor the criteria for full wakefulness. For this reason, we prefer a neurocognitive definition of sleep, as defined in the introductory sections of this thesis. This is following a line of research that, in the last decades, has revealed even cognitively complex tasks can sometimes be performed during unresponsive sleep (for a recent review see Andrillon & Kouider, 2020). For instance, Blume, et al. (2017) found differential processing to salient stimuli during N1 and N2 (e..g a person's own name), in what they refer to as the sentinel mod. Similarly, multiple studies have found semantic processing for single neutral words (Kouider, et al., 2014; Andrillon, et al., 2016).

This is in line with our MVPA results, which showed above chance classification of words by semantic identity, revealing that information processing still occurs during drowsiness, even after sleep deprivation. This is also supported by our behavioural findings, indicated by low error rates and the presence of a conflict effect across conditions, which is dependent on successful semantic processing.

Our findings are also in line Kouider et al. (2011), who reported that not only can stimuli be classified according to semantic category, but motor planning could still be initiated during N1/2, even in unresponsive trials. Overall, our findings confirm that semantic processing persists for single words during early sleep.

6.7 Information integration during the SOP

The persistence of behavioural conflict detection effect during drowsiness suggests that location and semantic content continue to be integrated during drowsiness. However, the lack of conflict adaptation suggests an impairment of

integration across time. This is in line with findings suggesting preserved processing for auditory stimuli on shorter timescales but impaired in longer timescales of several seconds (Strauss, et al., 2015).

A study by Strauss, et al (2015) compared mismatch negativity to local and global deviants based on Bekinschtein, et al. (2009). The task consisted of a modified oddball paradigm that consisted of presenting sequential tone stimuli with either global or local deviants. Using EEG mismatch negativity, they found auditory processing during N1, N2, and REM sleep for local but not for global deviants. This suggests that global integration is impaired during sleep.

Our conflict adaptation findings can also be explained using the global/local framework, with the conflict detection effect being the result of local processing, and conflict adaptation requiring access to the global workspace (Dehaene and Changeux, 2011). When global processes become impaired during the sleep onset period, this results in a specific conflict adaptation impairment.

While our finding is also possibly explained as a WM effect, we argue this is implausible, as holding one item for 3 seconds is considered to incur a very low WM load (De Fockert & Bremner, 2011). However, this possibility cannot be fully ruled out.

6.8 Conflict processing across states of consciousness

The first systematic studies on cognitive interference defined it in behavioural terms, as a function of reaction times and errors. Most famously, the experiments carried out by J. Ridley Stroop in 1935 investigated the effect of incongruent stimulus features on RTs by using different combinations of colour words and colour inks to produce what is now known as the Stroop task. The robust finding that higher RTs are reliably associated with the processing of incongruent stimuli became later known as the conflict effect, and has since

become widely studied in a wide variety of contexts ranging from addiction (Cox et al., 2006) to hypnosis (Raz et al., 2002).

Notably, the conflict effect as it was originally conceived requires the participant to be in a responsive state in order to measure their reaction to a presented stimulus. However, as methods to measure and analyse brain activity develop, the neural underpinnings of the conflict effect have become better understood (Cavanagh & Frank, 2014). With a reliable neural marker for conflict, it would be possible to investigate it without need for a behavioural response. So called no-report paradigms (Tsuchiya et al., 2015) have been advantageous in the study of consciousness because 1) they remove confounds associated with response production (e.g. motor planning, self-monitoring, etc) and 2) they enable the study of cognitive processes during unresponsive states, such as sleep, disorders of consciousness, and anaesthesia.

In a classic example of a no-report paradigm, Cruse and colleagues (2011) were able to detect awareness in vegetative state (VS) patients by recording brain activity during a motor imagery task. By decoding VS patients EEG activity, they were able to show that some patients had enough awareness to attend and follow verbal commands, as well as engage in motor imagery. While no studies have been conducted on conflict detection or conflict adaptation in DOCs, it would not be surprising that at least some VS patients would display a similar profile to that observed in awake healthy participants during conflict as measured by frontal theta.

6.9 Bottom-up vs top-down mechanisms

Recently, Gevers, et al. (2015) suggested the distinction between bottom-up and top-down control in the context of a modified Stroop task. In order to test this hypothesis, they included two types of incongruent trial pairs, where the stimuli were either identical (e.g. ROUGE-ROUGE), or incongruent but non-identical (e.g. ROUGE-VERT). They found that sleep deprivation affected conflict adaptation only when trials were not identical, which they interpreted as a specific effect on top-down control.

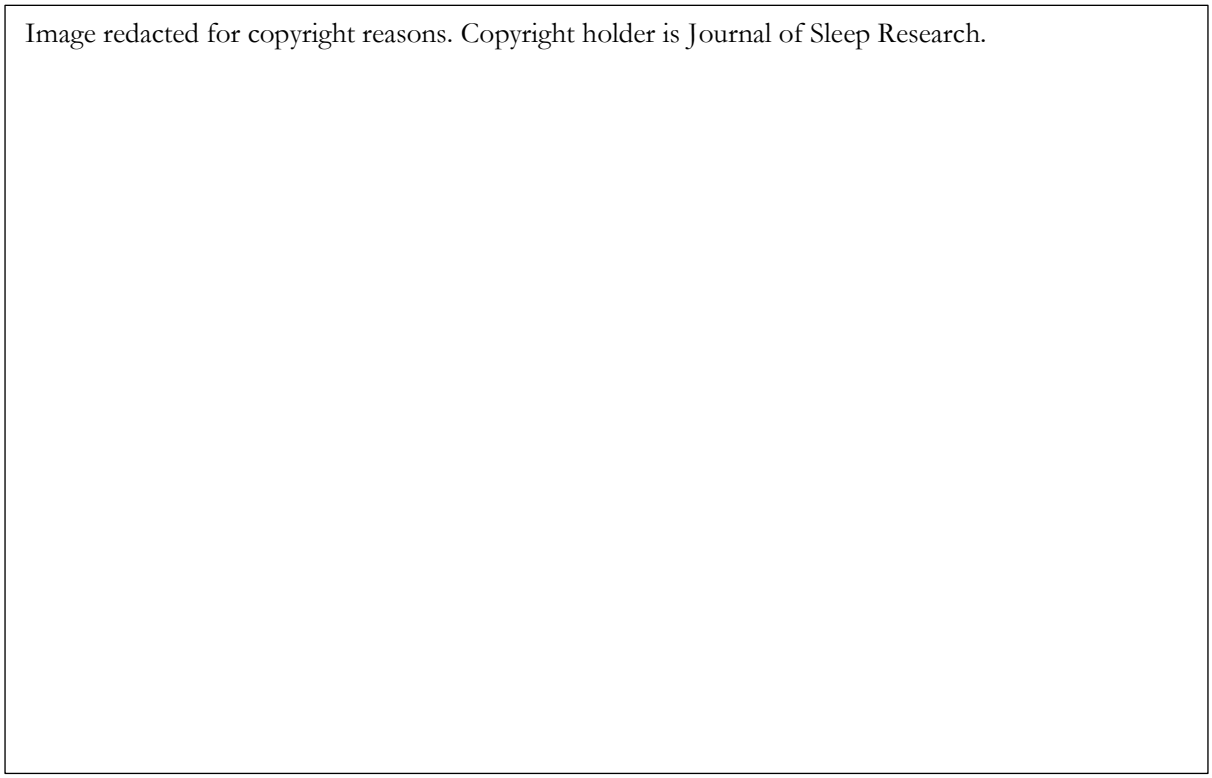

FIGURE 28. EFFECTS OF SLEEP DEPRIVATION ON BOTTOM-UP AND TOP-DOWN CONFLICT ADAPTATION (ADAPTED FROM GEVERS, ET AL., 2015). AN ADAPTATION EFFECT IS OBSERVED AFTER SLEEP DEPRIVATION IN BOTTOM-UP COGNITIVE CONTROL, BUT IS ABSENT WHEN TOP-DOWN PROCESSING IS REQUIRED.

Our conflict adaptation behavioural results look remarkably similar to their repetition (i.e. bottom-up) condition during wakefulness, and therefore are worth discussing. Given that our conflict adaptation condition did not differentiate between repeated and non-repeated incongruent stimuli, we cannot fully tease out

the effects of bottom-up from top-down processes. The loss of conflict adaptation during drowsiness could mean that bottom-up cognitive control is lost during reduced alertness, indicating Gevers, et al. (2015) finding might be unrelated to changes in alertness and rather a result of another mechanism linked to sleep deprivation.

The confounding of top-down and bottom-up mechanisms of control could also explain why we found no effect of sleep deprivation on conflict adaptation during wakefulness. However, an important difference between both studies is that in Gevers, et al. participants were totally sleep deprived for a night, while the present study only partially deprived participants (<4hrs). Therefore, the presence of conflict adaptation during sleep deprived wakefulness might also reflect a "dose-dependent" effect of sleep deprivation.

6.10 Time and consciousness: back to phenomenology

"The experience of temporality addresses head-on the fundamental fact that we exist only within a transparent web of time"

- Francisco Varela, 1999

The findings presented in this thesis are aligned with theories that suggest consciousness has a functional role, connecting the past (learning), present (behaviour), and future (the realisation of goals) into a cohesive frame of reference for goal-directed action (e.g. Husserl, 1964). It might be the case that the rapid and unstable changes in alertness that occur during the SOP result in the breakdown of temporality and thus limit the functional utility of consciousness: fast and flexible behaviour.

6.11 Future directions

In the set of studies presented, I have sought to characterise the dynamic cognitive processes that accompany the transition from wakefulness to sleep.

Furthermore, I have argued that understanding the effect of alertness on cognitive control might help us tell apart between the processes that require consciousness and those that do not. However, there are still many questions to ask.

6.11.1 What about unresponsiveness?

Along the introduction and discussion sections thesis, I summarised multiple studies that investigated brain activity during unresponsive sleep. However, in all of the experimental setups developed for this thesis, we sought to maximise our behavioural data by waking up participants whenever they stopped responding. This means some questions regarding information processing during deeper stages of sleep have been left unanswered.

Winter (1995) hypothesised that "during light sleep, scanning of the environment is performed by a different system than in the awake state and that during drowsiness a gradual switch between these two systems takes place." Under this hypothesis, we might expect that even though stimulus congruency could not be decoded during drowsiness using our MVPA approach, it might once again emerge during later stages of N1/N2 which are likely underrepresented in our sample. This would be compatible with the finding from Canales-Johnson, et al. (2020) of an increase in long-range connectivity associated with conflict during drowsiness.

6.11.2 Disentangling working memory from cognitive control

As we covered in the discussion, we cannot fully rule out the possibility that our conflict adaptation effects are rather the result of WM impairments during drowsiness. This could be investigated by testing whether working memory interacts with conflict adaptation during drowsiness. Impaired conflict adaptation as a result

of increase working memory load would indicate that resources are shared between both processes.

6.11.3 Exploring errors

Trends in error rates appear to reflect a similar pattern than that observed in reaction times. However, given that performance was nearly at 100% accuracy, analysing errors under the current task is likely to exhibit a positive bias, meaning just a single error will make a much bigger difference than it normally would, as error rate variance is not being accurately measured.

A way to circumvent this would be to make the task slightly more difficult, for example by introducing a time limit (at the cost of interpretability of RT data and potentially a large number of missed trials in the drowsy condition). A possible hypothesis is that participants make more errors during incongruent than congruent trials (i.e. a main effect of congruency) as well as more mistakes in the drowsy condition (a main effect of alertness). However, this might also reveal an interaction between congruency and alertness that was not seen in RTs, indicating a cognitive cost of further top-down pressures to respond on time.

Furthermore, adding a time limit would reduce the variability in the EEG signal and thus make the neural activity in our drowsy trials more comparable to awake condition.

6.11.4 Does sleep deprivation really have no effect on adaptation?

Here, we investigated the effects of partial sleep deprivation on neurobehavioural markers of cognitive control. We expected to find no effects of sleep deprivation on conflict detection, as has been widely reported from findings in the Stroop effect (Bratzke, et al., 2012; Cain et al., 2011). However, informed by findings that suggested selective effects of deprivation in specific cognitive control subfunctions, (Gevers, et al., 2015; Slama, et al., 2018), we expected conflict adaptation to be impaired as a result of sleep deprivation.

The fact that we did not observe an interaction between sleep deprivation and conflict adaptation may be have a cognitive explanation (discussed in Section 6.8), however it might also be the case that our manipulation was not strong enough to impair conflict adaptation, and that total sleep deprivation may have yielded different results. It has indeed been found that the effect of sleep deprivation on sustained attention is dependent on the amount deprivation (Lo, et al., 2012).

Furthermore, while the effects of acute sleep deprivation have been widely investigated , there is still more to understand regarding the long-term effects of chronic sleep deprivation.

6.11.5 How is frontal disinhibition related to spontaneous imagery and creativity?

To explain the trade-off between goal-oriented thinking and mind-wandering, Sripada (2018) has suggested an exploration/exploitation framework, where controlled and targeted processes of goal-orientedness are balanced against the less restrictive processes associated with mind-wandering in order to obtain the biggest environmental rewards. He proposes an 'oscillatory strategy' where explorative vs exploitative behaviour switch back and forth at the scale of minutes to seconds in order to provide the most optimal strategy for environmental adaptability.

Under this framework, the SOP could be thought of as a maximally variable state where cognition becomes biased towards exploration, and exploitation thought becomes minimised, giving rise to the intense mind-wandering that results in dream-like mentation. Inevitably, the exploration/exploitation trade-off results in goal-directed behaviour becoming impaired. Such experiences are widely reported across the literature (for a review, see Nielsen, 2017) and commonly alluded to in folk psychology and art.

A task where participants are asked to perform a cognitive control task could be complemented by prompting participants to provide a subjective report about

their thoughts right at the onset of unresponsiveness. The oscillatory strategy hypothesis would suggest that it is in this moment when mind-wandering processes could more readily emerge.

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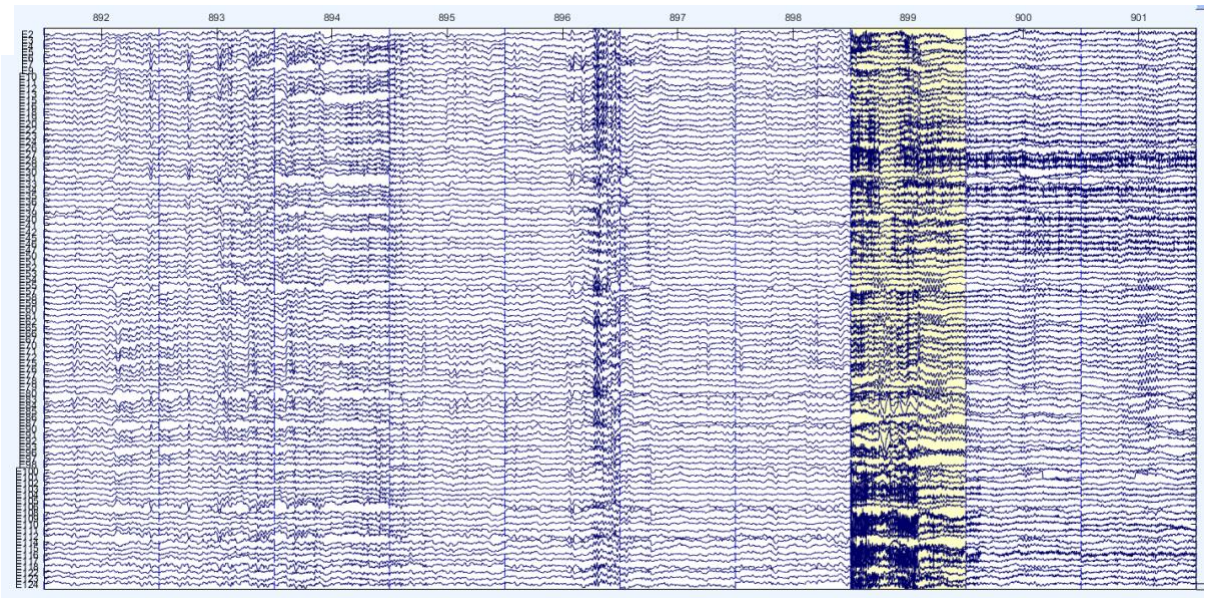
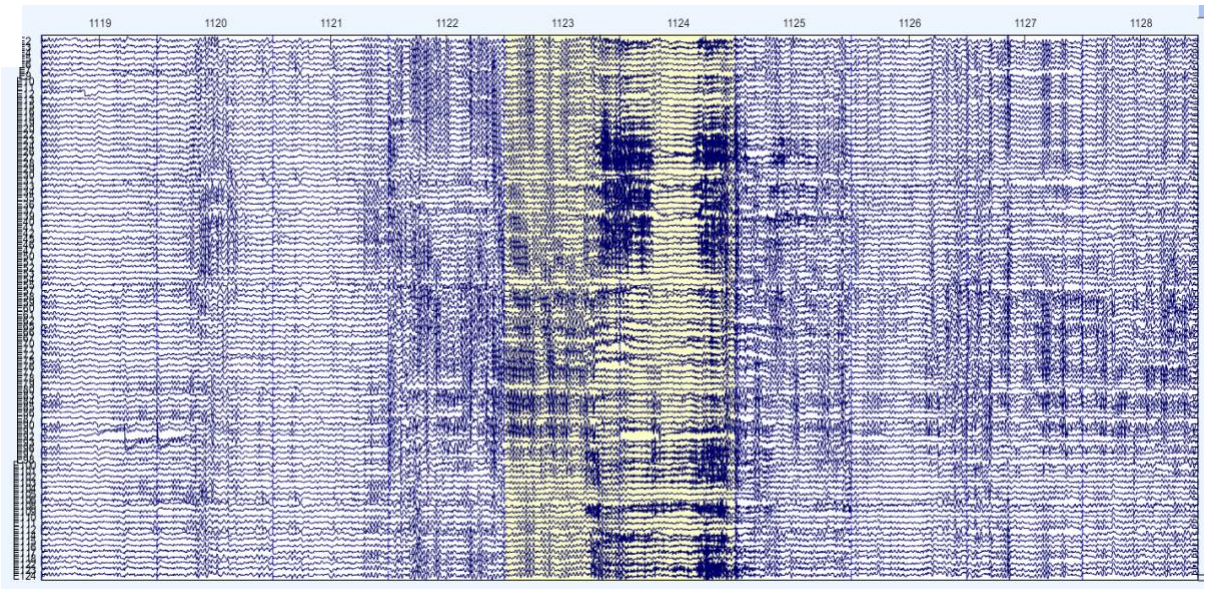
Appendix A. Bad trial rejection

1



2



The figures above above show two epoched samples from different participants in our conflict task, although the same criteria was employed in the Go/NoGo task. Trial 899 for participant 1 and trials 1123 and 1124 for participant 2 were rejected. Scale shown at 30uV.

Appendix B. Sleepiness questionnaire administered to participants

Epworth Sleepiness Scale

Name	Click here to enter text.	Sex	Click here to enter text.
Age	Click here to enter text.	Date	Click here to enter text.

How likely are you to doze off or fall asleep in the following situations, in contrast to feeling just tired? This refers to your usual way of life in recent times. Even if you have not done some of these things recently, try to work out how they would have affected you.

Use the following scale to choose the most appropriate answer for each situation.

0 – would never doze
1 – slight chance of dozing
2 – moderate chance of dozing
3 – high chance of dozing

SITUATION	CHANCE OF DOZING
Sitting and reading	score
Watching TV	score
Sitting, inactive in a public place – e.g. a theater or a meeting	score
As a passenger in a car for an hour without a break	score
Lying down to rest in the afternoon circumstances permit	score
Sitting and talking to someone	score
Sitting quietly after lunch without alcohol	score
In a car, while stopped for a few minutes in traffic	score
TOTAL SCORE	score